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# INTERRELATIONSHIPS OF AND WITHIN *BREVIRAJA* BASED ON ANATOMICAL STRUCTURES (PISCES: RAJOIDEI)

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## ABSTRACT

Claspers, neurocrania, scapulocoracoids and vertebral numbers of 11 of the 12 species currently classified in *Breviraja* were compared with each other and with those of *Raja* subgenera thought to be related to *Breviraja*. On its rostral morphology, *B. yucatanensis* was reallocated to the genus *Raja*. The remainder of *Breviraja*, including an undescribed species discovered during the study, consists of three morphological groups, possesses a number of derived character states for rajoids and, as presently constituted, is paraphyletic. The first group, consisting of *B. colesi* and *B. spinosa*, is the apomorphic sister group of *Raja* (*Leucoraja*). The second group, *B. caerulea*, *B. stehmanni* and *B.* sp., is the apomorphic sister group of *Raja* (*Malacoraja*). The third group, *B. sinusmexicanus*, *B. sibogae*, *B. ishiyamai*, *B. cubensis*, *B. plutonia* and *B. atripinna*, plus *Gurgesiella*, is the apomorphic sister group of the second group. *Gurgesiella* is the apomorphic sister group of the third group. Present information is not sufficient to determine the interrelationships within the second group. Interrelationships within the third group are tentative because of specific variation and paucity of synapomorphies. *B. sinusmexicanus* and *B. sibogae* share one synapomorphic and two plesiomorphic character states suggesting that they are sister species. The other four species share a synapomorphic character state suggesting that they, plus *Gurgesiella*, form the apomorphic sister group of *B. sinusmexicanus* and *B. sibogae*. *B. cubensis*, *B. plutonia*, *B. atripinna* and *Gurgesiella* share a synapomorphy suggesting that they form the apomorphic sister group of *B. ishiyamai*. *B. cubensis* and *B. plutonia* share two synapomorphies suggesting that they are sister species. *B. atripinna* possesses an autapomorphy and two synapomorphies with *Gurgesiella* suggesting that it plus *Gurgesiella* form the apomorphic sister group of *B. cubensis* and *B. plutonia*. Interrelationships of the three groups of *Breviraja* necessitate the restriction of *Breviraja* to the first group, *B. colesi* and *B. spinosa*; and the erection of a new genus, *Neoraja*, and two subgenera, *Neoraja* and *Fenestraja* for the second and third groups.

Although the rajoid genus *Breviraja* Bigelow and Schroeder, 1948 was only recently erected, its species composition and definition have varied considerably since its inception. Bigelow and Schroeder (1948) proposed *Breviraja* for their new species *B. colesi* (the type-species of the genus) and *B. plutonia* (Garman, 1881), both from the western North Atlantic. They defined *Breviraja* as: "Rajidae with a rostral cartilage, but with the latter falling considerably short of the extremities of the anterior rays of the pectorals and hence short of the tip of the snout; the anterior pectoral rays of the two sides are either close together anteriorly or are farther separated. Characters otherwise as in *Raja*." Bigelow and Schroeder (1950) described five new species of *Breviraja* from the western North Atlantic, *B. cubensis*, *B. atripinna*, *B. sinusmexicanus*, *B. spinosa*, and *B. yucatanensis*; and later (Bigelow and Schroeder, 1962), described yet another, *B. ishiyamai*.

Examination of the rostral structure of new and previously described species of skates from outside the western North Atlantic area led Ishiyama (1952; 1958; 1967), de Buen (1959; 1960), Bigelow and Schroeder (1965), Forster (1967), and Krefft (1968) to place a host of additional species in *Breviraja*, including: *B. tobitukai* (Hiyama, 1940), *B. isotrachys* (Günther, 1877), *B. trachouros* Ishiyama,

1958, *B. violacea* (Suvorov, 1935), *B. diplotaenia* (Ishiyama, 1950), *B. matsubarai* Ishiyama, 1952, *B. aleutica* (Gilbert, 1896), *B. parmifera* (Bean, 1882), *B. simoterus* Ishiyama, 1967, and *B. smirnovi* (Soldatov and Pavlenko, 1915), from the western North Pacific off Japan and adjacent areas; *B. longicauda* de Buen, 1959 and *B. nigerrima* de Buen, 1960, from the eastern South Pacific off Chile; *B. spinicauda* (Jensen, 1914) and *B. pallida* Forster, 1967, from the North Atlantic; *B. brachyurops* (Fowler, 1935), *B. griseocauda* (Norman, 1937), *B. scaphiops* (Norman, 1937), *B. albomaculata* (Norman, 1937), *B. macloviana* (Norman, 1937), *B. magellanica* (Steindachner, 1903), and *B. schroederi* Krefft, 1968, from the western South Atlantic; and *B. eatonii* (Günther, 1876), from off Kerguelen Island in the subantarctic Indian Ocean.

Ishiyama and Hubbs (1968) compared the rostral structure and claspers of *Breviraja colesi* with the western North Pacific skates previously placed by Ishiyama (1958; 1967) in *Breviraja*. They found that the Pacific skates were phylogenetically and morphologically distinct from *Breviraja* (as characterized by them from *B. colesi*), and merited a separate genus, *Bathyraja* Ishiyama, 1958 (raised in rank from a subgenus of *Breviraja*). They also stated that Bigelow and Schroeder (1948) were incorrect in claiming that the rostral cartilage of *Breviraja* failed to reach the snout tip because the rostral shaft extends to the rostral node as a slender, uncalcified rod in *B. colesi*. Following the account of Ishiyama and Hubbs (1968), the species previously placed in *Breviraja* from the North Atlantic, western South Atlantic, and Indian Ocean were transferred to *Bathyraja* (Stehmann, 1970; 1978; Hulley, 1970; Menni, 1972). Our examination of specimens of most of these species and those from the western North Pacific confirms their placement in *Bathyraja* (or more properly, its senior synonym *Thetaraia* Leigh-Sharpe, 1924). Stehmann (1970) and Hulley (1972a) stated that *Breviraja* was restricted to the continental slopes of the tropical western Atlantic, thus implying that all *Breviraja* species from other areas should be removed from this genus. However, recent work by the same writers indicates that *Breviraja sensu* Bigelow and Schroeder (1948; 1950; 1953; 1962) does occur outside of the western Atlantic. Hulley (1972b) described a new species, *B. stehmanni,* from the southeastern Atlantic, while Stehmann (1976a) placed two previously described species from the Indian Ocean, *B. mamillidens* (Alcock, 1889) and *B. sibogae* (Weber, 1913) in the genus and also Stehmann (1976b) named a new species, *B. caerulea,* from the eastern North Atlantic.

*Breviraja* currently consists of 12 described and at least one undescribed species (*B. atripinna, B. colesi, B. cubensis, B. ishiyamai, B. plutonia, B. sinusmexicanus, B. spinosa, B. yucatanensis* and *B.* sp. from the western North Atlantic; *B. caerulea* from the eastern North Atlantic; *B. stehmanni* from the eastern South Atlantic; and *B. mamillidens* and *B. sibogae* from the northern Indian Ocean). The undescribed species was discovered during the course of this study and will be described fully elsewhere after additional material has been examined. Two or three species may be added to the genus when adequate material becomes available. The two *Breviraja* described by de Buen (1959; 1960) from Chile includes one, *B. nigerrima,* that on the basis of its anatomical characters should be classified in the *Raja* subgenus *Malacoraja*; but the placement of the other, *B. longicauda,* remains uncertain because the species has not been reported since de Buen's original description and the holotype and only known specimen has apparently been lost (R. J. Lavenberg, *pers. comm.*). De Buen's description and illustration are inadequate to determine if *B. longicauda* is a member of *Breviraja, Bathyraja,* or some other genus. Stehmann (1976a) found that three specimens from the western Indian Ocean identified by Weber (1913) as *Raja mamillidens* Alcock, 1889 (=*Breviraja mamillidens*) were members of

*Breviraja* but not *B. mamillidens*. However, the three specimens were immature and in poor shape so Stehmann refrained from describing a new species for them. Stehmann (1976b) stated that a skate specimen from the northeastern Atlantic identified by Vaillant (1888) as *Raja fullonica* Linnaeus, 1758 represented another undescribed species of *Breviraja*, but Stehmann again did not name it because of the poor condition of the only specimen.

To date, detailed anatomical descriptions of characters important in classifying rajoids (Ishiyama, 1958; Stehmann, 1970; Hulley, 1972a; McEachran and Compagno, 1979) have been published for three species of *Breviraja*: *B. stehmanni* (Hulley, 1972b); *B. sibogae* and *B. caerulea* (Stehmann, 1976a; 1976b). Although several studies have presented hypotheses on the phylogenetic affinities of *Breviraja*, too little is known of the variability of character states within the genus to ascertain its relationships with other rajoid taxa. Also, the relationships within the genus are unknown.

The purposes of the present study are to compare anatomical characters important in rajoid classification in all available species of *Breviraja*, to work out the phylogeny of the species, and compare them with other rajoids, to determine the phylogenetic relationships of *Breviraja* with other rajoid taxa.

## Materials and Methods

Specimens of 12 of the 13 *Breviraja* species (*B. atripinna, B. caerulea, B. colesi, B. cubensis, B. ishiyamai, B. plutonia, B. sibogae, B. sinusmexicanus, B. spinosa, B. stehmanni, B. yucatanensis* and *B.* sp.) were examined and compared with species of the *Raja* subgenera *Leucoraja, Malacoraja* and *Rajella*, all thought to be closely related to *Breviraja* (Hulley and Stehmann, 1977; Stehmann, 1977; Compagno and McEachran, in prep.). The type and only known specimen of the thirteenth species, *B. mamillidens*, has been lost (Stehmann, 1976a). *Breviraja* was compared with *Raja* (*Leucoraja*) *clarki*, *R.* (*L.*) *erinacea*, *R.* (*L.*) *ocellata*, *R.* (*Malacoraja*) *fuliginea*, *R.* (*M.*) *nigerrima*, *R.* (*M.*) *senta*, *R.* (*Rajella*) *bigelowi*, *R.* (*R.*) *fyllae* and *R.* (*R.*) *leopardis*. *R. fuliginea*, *R. nigerrima* and *R. senta* are placed in *Malacoraja* because of the great similarity of their claspers, neurocrania, external shape and spination with those of *R.* (*M.*) *kreffti* and *R.* (*M.*) *spinacidermis* (Compagno and McEachran, in prep.). Type material was included for all species except *B. stehmanni*, *R. erinacea*, *R. ocellata*, *R. fyllae*, *R. nigerrima*, *R. leopardis* and *R. senta*. Specimens examined were borrowed from the Aussenstelle Ichthyologie des Institut für Seefischei, Hamburg (ISH); Florida State Museum (FSM); Museum of Comparative Zoology (MCZ); National Museum of Natural History, Smithsonian Institution (USNM); Smithsonian Oceanographic Sorting Center (SOSC); Texas A&M University Systematic Collection of Marine Organisms (TAMU); Texas Cooperative Wildlife Collection (TCWC); University of Miami Rosenstiel School of Marine and Atmospheric Science (UMML); Virginia Institute of Marine Science (VIMS); and Zoologisch Museum Universiteit van Amsterdam (ZMA). A list of material examined follows the text.

One or, when available, two specimens of each species were dissected to remove the neurocranium and left scapulocoracoid and to expose cartilages of the right clasper. *Breviraja yucatanensis* was only partially dissected because only one specimen, the holotype, was available for study. Dissection was limited to exposing the rostral cartilage. Additional specimens of each species were radiographed to verify anatomical observations based on dissections and to count trunk and predorsal tail vertebrae.

External measurements were made according to methods of Bigelow and Schroeder (1953). Krefft (1968) was followed in counting vertebrae from radiographs. Clasper terminology followed Stehmann (1970; 1976a) and Hulley (1972a) and cranial and scapulocoracoid terminology followed McEachran and Compagno (1979). Neurocranial measurements were based on methods of Hubbs and Ishiyama (1968) as modified by McEachran and Compagno (1979).

The phylogenetic relationships were constructed according to the cladistic method of grouping taxa by synapomorphy as outlined by Henning (1966). Derived (apomorphic) character states and character polarities for the species studied were determined by comparing character states with those of other rajoid taxa and with those of the postulated plesiomorphic sister group of the rajoids (rhinobatoids).

## Results

*Aspects of External Morphology*.—Most species of *Breviraja* possess oronasal pits and several possess a ventral (hypochordal) caudal lobe at the tip of the tail, although these character states were apparently overlooked by previous investi-

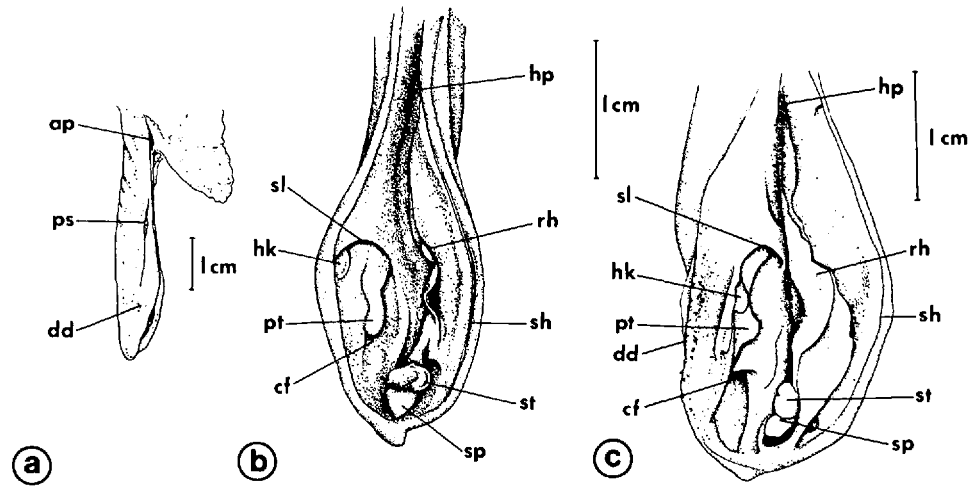


Figure 1. a, b. Right clasper of *Breviraja colesi* MCZ 41158. a, dorsal view; b, lateral view opened to show components. c. Right clasper of *B. spinosa* MCZ 40232, lateral view opened to show components. ap—apopyle, cf—cleft, dd—dermal denticles, hk—hook, hp—hypopyle, ps—pseudosiphon, pt—promontory, rh—rhipidion, sh—shield, sl—slit, sp—spike, st—sentinel.

gators. The oronasal pit, which was lacking only in *B. caerulea, B. stehmanni, B.* sp. and *B. yucatanensis,* resembles that described for *Pseudoraja fischeri* (Bigelow and Schroeder, 1954). A pit is located ventrally on either side dorsal to the nasal curtain, between the upper jaw and posterior margin of the nasal capsule. In *B. colesi* and *B. spinosa* the pits are directed dorsomedially. In *B. sinusmexicanus, B. sibogae, B. ishiyamai, B. plutonia, B. cubensis,* and *B. atripinna* the pits are more laterally positioned than in *B. colesi* and *B. spinosa* and are directed dorsolaterally.

Hypochordal lobes with fin rays occur in *B. stehmanni, B. caerulea, B.* sp. and *B. atripinna.* The hypochordal lobe extends from just anterior to the termination of the lateral caudal fold to the tip of tail. Its height in the above species varies from about one-fourth to about equal to height of epichordal lobe. The epichordal and hypochordal lobes are not confluent at tip of tail in any of the species.

*Claspers.*—Claspers of 10 of the 12 available species of *Breviraja* were examined (mature males were not available for *B. yucatanensis* and *B.* sp.) and these could be grouped into three morphological groups. Below each type is described and interspecific variation is discussed.

GROUP I. Clasper of *B. colesi* (Fig. 1a) is relatively stout, with dermal denticles along dorsal margin and on dorsal surface of clasper shaft; with pseudosiphon formed entirely by dorsal dilatator muscle; inner dorsal lobe with hook (new term for a movable cartilaginous process curved toward tip of glans, formed by dorsal terminal 3 cartilage), which corresponds to promontory of Ishiyama and Hubbs (1968), located near dorsal margin of glans (Fig. 1b); promotory distomedial to hook; cleft situated distal to promontory; ventral lobe with well developed shield extending length of glans, possessing sharp and naked lateral margin; rhipidion extending from level of hypopyle to level of sentinel; sentinel distally located and foot-shaped; spike distal to sentinel. Dorsal terminal 1 cartilage (Fig. 2a) strap-shaped and diagonal to axis of clasper, partially covering distal section of dorsal

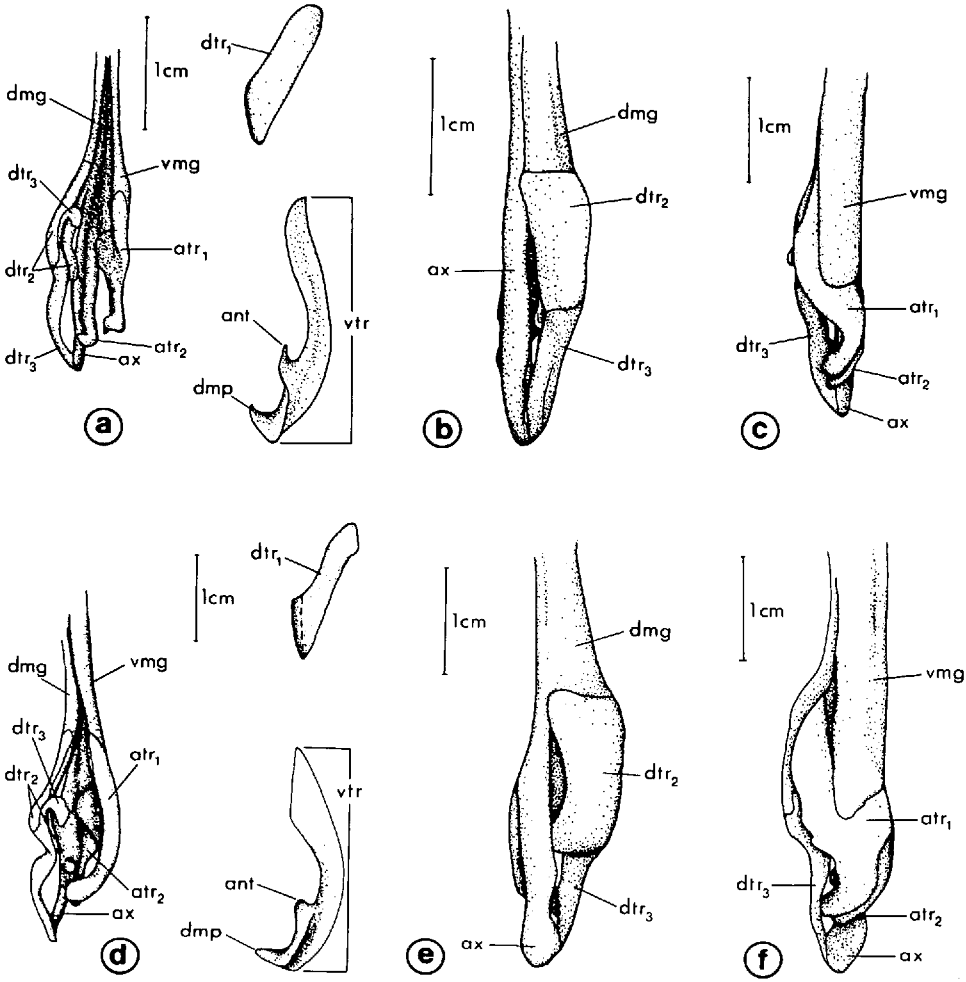


Figure 2. a, b, c. Right clasper cartilages of *Breviraja colesi* MCZ 41158. a, lateral view partially expanded; b, dorsal view; c, ventral view. d, e, f. Right clasper cartilages of *Breviraja spinosa* MCZ 40232. d, lateral view partially expanded; e, dorsal view; f, ventral view. ant—anterior notch, $atr_1$—accessory terminal 1 cartilage, $atr_2$—accessory terminal 2 cartilage, ax—axial cartilage, dmg—dorsal marginal cartilage, dmp—distal medial process, $dtr_1$—dorsal terminal 1 cartilage, $dtr_2$—dorsal terminal 2 cartilage, $dtr_3$—dorsal terminal 3 cartilage, vmg—ventral marginal cartilage, vtr—ventral terminal cartilage.

terminal 2 and dorsal aspect of axial; dorsal terminal 2 truncate with distomedial extension forming promontory, attached to distal margin of dorsal marginal (Fig. 2b); dorsal terminal 3 rather slender, attached to distomedial surface of dorsal terminal 2 and to distal tip of axial, with a proximal recurved process forming hook; ventral terminal very slender, J-shaped, with an anterior notch and distomedial process wrapping around distal aspect of axial; accessory terminal 1 Y-shaped, attached to distal and distolateral margins of ventral marginal, with distal curved extension forming sentinel (Fig. 2c); accessory terminal 2 rod-shaped, attached to distal margin of ventral marginal between axial and accessory terminal 1, with distal extension forming spike.

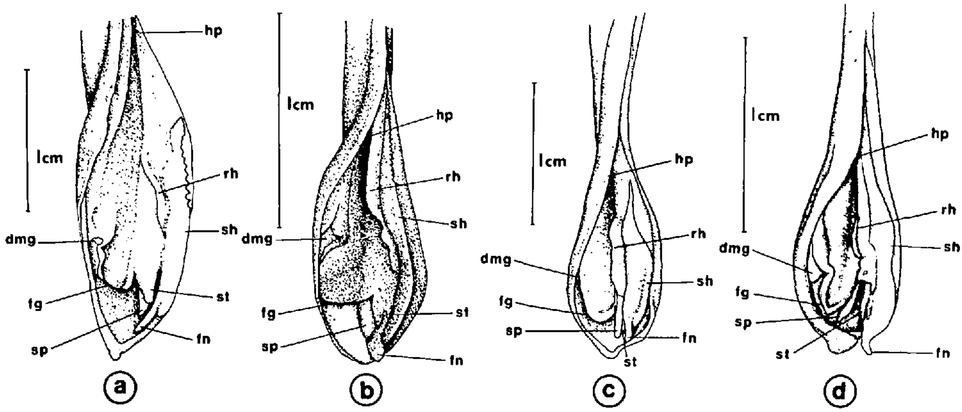


Figure 3. Lateral view of right clasper opened to show components. a, *Breviraja sinusmexicanus* TCWC 2696.1; b, *B. cubensis* MCZ 41928; c, *B. plutonia* TCWC 2734.1; d, *B. atripinna* MCZ 41828. dmg—dorsal marginal cartilage, fg—flag, fn—funnel, all other anatomical abbreviations defined in Figure 1.

Clasper of *B. spinosa* (Fig. 1c) is similar to that of *B. colesi* but is stouter and possesses a more strongly developed pseudosiphon, cleft and promontory. Ventral terminal is more acutely pointed and expanded than in *B. colesi* (Fig. 2d,e,f). Axial possesses lateral protuberance which abutts against dorsal terminal 3.

GROUP II. Claspers of *B. caerulea* and *B. stehmanni* were described by Stehmann (1976b) and Hulley (1972b) respectively, and are closer to each other than either is to claspers of any other *Breviraja* species which were studied. Shared character states include: (1) terminal bridges separating proximal and distal clefts; (2) well developed shields; (3) proximally located, finely pitted rhipidia; (4) well developed dikes; (5) dorsal marginal cartilages with distomedial extensions forming pseudorhipidion-like structures; (6) dorsal terminal 1 cartilages with proximal extensions; (7) ventral terminal cartilages with anterior notches; (8) ventrally united dorsal terminal 1 and ventral terminal cartilages; (9) U-shaped accessory terminal 1 cartilages with Z-shaped lateral projections; and (10) accessory terminal 2 cartilages with spatula-like distal extremities.

GROUP III. *B. sinusmexicanus, B. sibogae, B. ishiyamai, B. cubensis, B. plutonia* and *B. atripinna* have claspers displaying only subtle individual variations, which in some cases, could be used to suggest interrelationships within the group. All species possess clasper components flag and funnel, lack dorsal terminal 1 cartilages and possess dorsal marginal cartilages with distolateral margins which project into medial surface of the dorsal lobe of glans, immediately distal to lateral margin of flag.

The clasper of *B. sinusmexicanus* (Fig. 3a) is moderately slender without dermal denticles or pseudosiphon; inner dorsal lobe with flag running from distal third of glans to near tip of sentinel; shield with naked lateral margin, serrated proximally and sharp-edged distally; rhipidion extending from level of proximal tip of shield to distal third of glans; sentinel distally located with naked acutely pointed tip; spike distal to sentinel, chisel-shaped, with naked and sharp-edged margin; funnel distal to spike, narrow with acutely pointed tip. Dorsal marginal with free distolateral extension entering glans (Fig. 4a); dorsal terminal 1 lacking; dorsal terminal 2 attached to distolateral surface of dorsal marginal, with distal

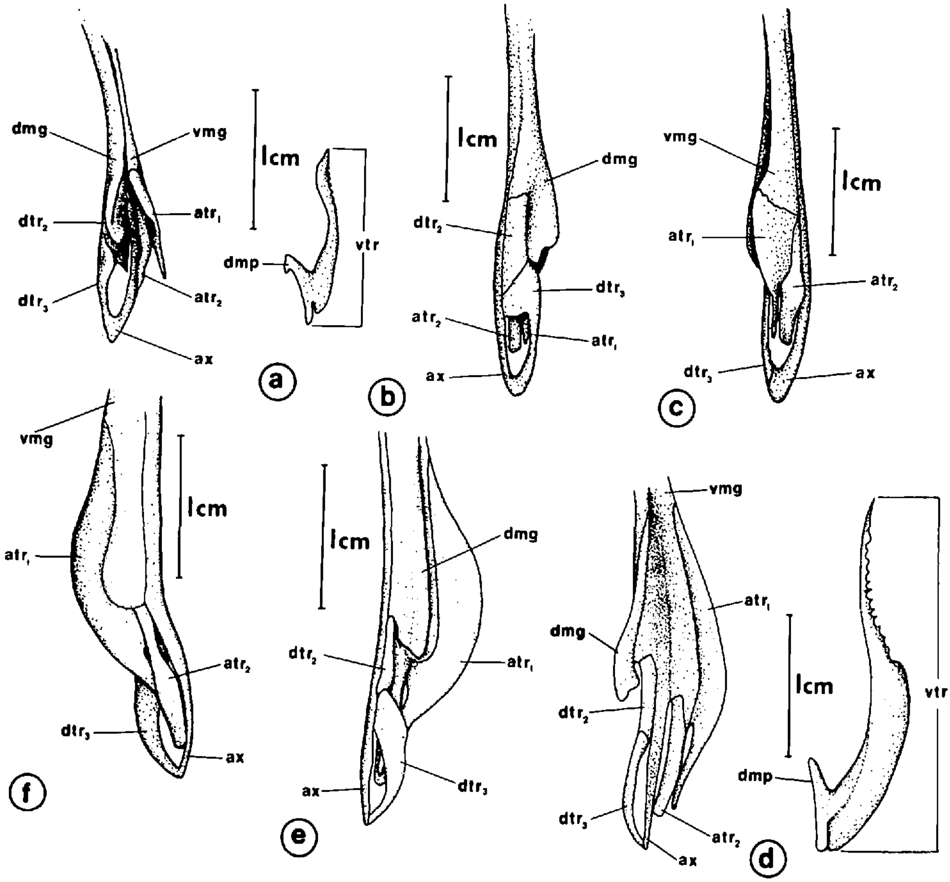


Figure 4. a, b, c. Right clasper cartilages of *Breviraja sinusmexicanus* TCWC 2696.1. a, lateral view partially expanded; b, dorsal view; c, ventral view. d, e, f. Right clasper of *B. sibogae* ZMA 113.491. d, lateral view partially expanded; e, dorsal view; f, ventral view. Anatomical abbreviations defined in Figure 2.

margin diagonal to long axis of clasper and attaching to dorsal terminal 3 (Fig. 4b); dorsal terminal 3 narrowing distally, forming band-like connection with tip of axial; ventral terminal check-shaped, proximal shaft slender and serrated, without anterior notch, distal extension forming funnel, distomedial process wrapping around accessory terminal 2 and meeting axial; accessory terminal 1 attached to distal border of ventral marginal, with simple distal extension forming sentinel (Fig. 4c); accessory terminal 2 attached to distal margin of ventral marginal, between accessory terminal 1 and axial, with straight sharp-edged distal margin forming spike.

Clasper of *B. sibogae* shares two character states with that of *B. sinusmexicanus,* which are considered plesiomorphic for group III, i.e. claspers are moderately splayed out at origin of glans (Stehmann, 1976b, Fig. 5) and proximal arm of accessory terminal 1 lies on lateral margin of the ventral terminal (Fig. 4d,e,f). However, *B. sibogae* is distinguished from the other species in possessing relatively long ventral terminal and accessory terminal 1 cartilages, with accessory terminal 1 forming entire margin of ventral lobe of glans. The remaining four

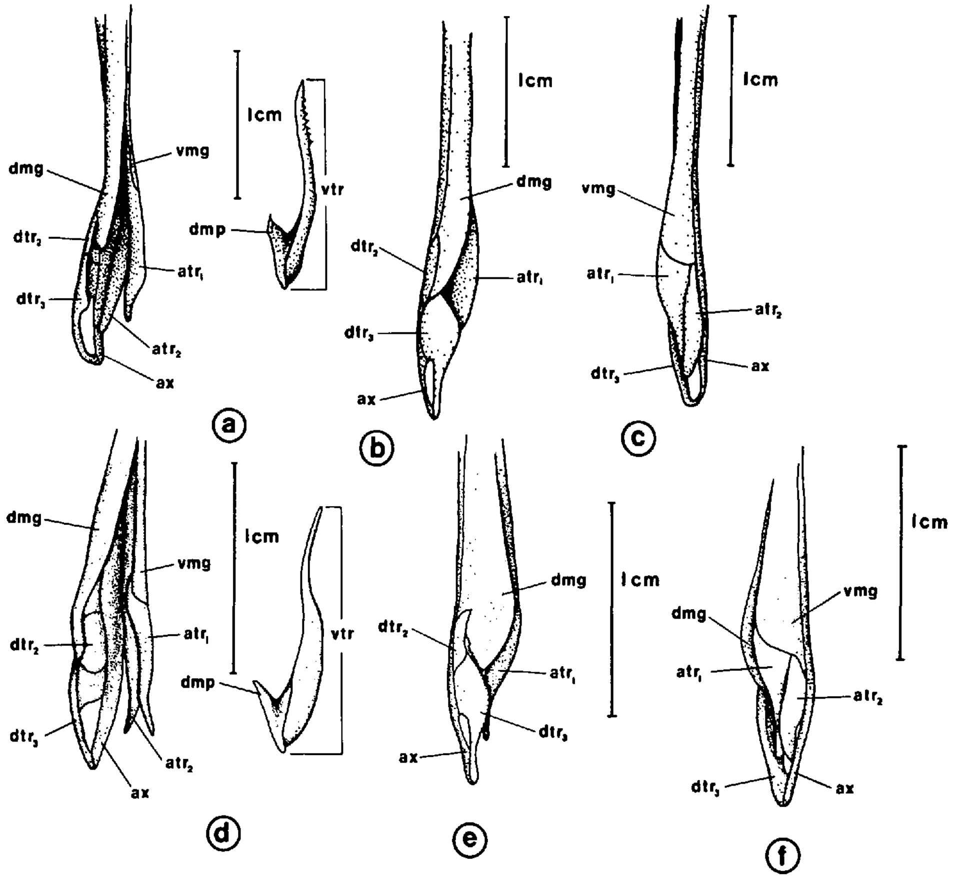


Figure 5. a, b, c. Right clasper cartilages of *Breviraja cubensis* MCZ 41928. a, lateral view partially expanded; b, dorsal view; c, ventral view. d, e, f. Right clasper cartilages of *B. plutonia* TCWC 2734.1. d, lateral view partially expanded; e, dorsal view; f, ventral view. Anatomical abbreviations defined in Figures 2 and 3.

species possess very slender claspers (Figs. 3, 5, 6) with tapering proximal extensions of accessory terminal 1 cartilages which curve medially and run along dorsal surface of ventral marginal. The latter character state is considered unique for Rajoidei. Claspers of *B. ishiyamai*, *B. cubensis* and *B. plutonia* are very similar except that ventral terminal of *B. plutonia* lacks serrations on proximolateral margin and dorsal terminal 2 and accessory terminal 2 of *B. ishiyamai* are relatively broad. Clasper of *B. atripinna* is distinct from all those of the above species in shape of distal medial process of ventral terminal cartilage (Fig. 6), and in possessing a dorsal marginal with a relatively short distolateral extension and a finger-like projection which enters the medial aspect of dorsal lobe of glans.

*Neurocrania.*—Based on the structure of the neurocrania the eleven species which were available for study could be grouped into the same morphological groups as determined from clasper structure.

GROUP I. Neurocranium of *B. colesi* has a rostral shaft which is greatly tapered proximally (Fig. 7a), at about midlength it is segmented and forms a slender rod

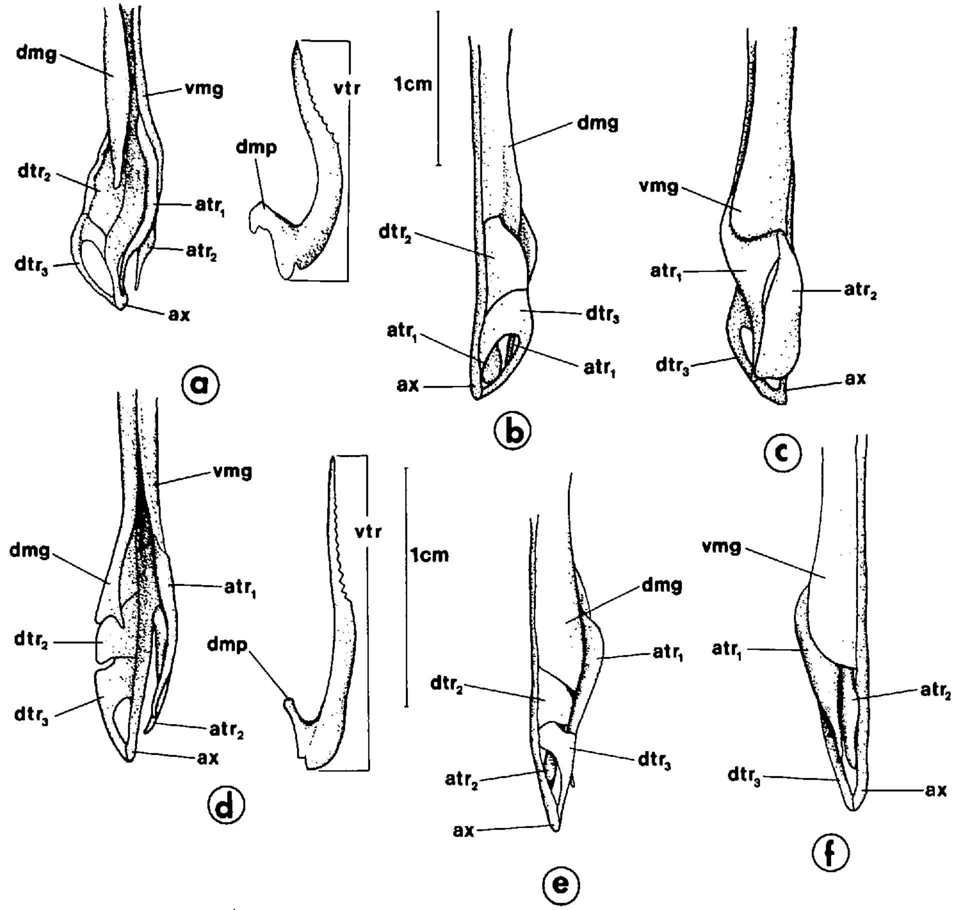


Figure 6. Right clasper cartilages of *B. ishiyamai* UMML 31682. a, lateral view partially expanded; b, dorsal view; c, ventral view. d, e, f. Right clasper cartilages of *B. atripinna* MCZ 41828. d, lateral view partially expanded; e, dorsal view; f, ventral view. Anatomical abbreviations defined in Figures 2 and 3.

just distal to segment which joins rostral appendices at tip of snout across a narrow bridge, representing rostral node; rostral appendices greatly enlarged and laterally expanded, free from rostral shaft over most of length, posteriorly almost reaching level of rostral segment, flattened over entire length; pectoral radials anteriorly reaching level of rostral node; rostral base relatively broad; nasal capsules narrow but laterally expanded, set at about 80° angle to long axis of neurocranium, rhomboidal in shape with antorbital condyles along lateral extremities; foramen for profundus nerve near leading edge of nasal capsule; anterior foramen for preorbital canal located dorsally at junction of nasal capsule and rostral base; internasal septum rather broad; interorbital region rather narrow; preorbital process well developed, separated from supraorbital crest by shallow groove; postorbital process well developed and bifurcated distally; anterior fontanelle broad, tear-shaped; posterior fontanelle narrow, shaped like a figure 8; foramen for otic branch of facial nerve medial to postorbital process; posterior foramen for preorbital canal on anterodorsal aspect of orbit (Fig. 7b); orbitonasal canal on anteroventral aspect of orbit; optic nerve foramen anterior to midline of orbit; foramen

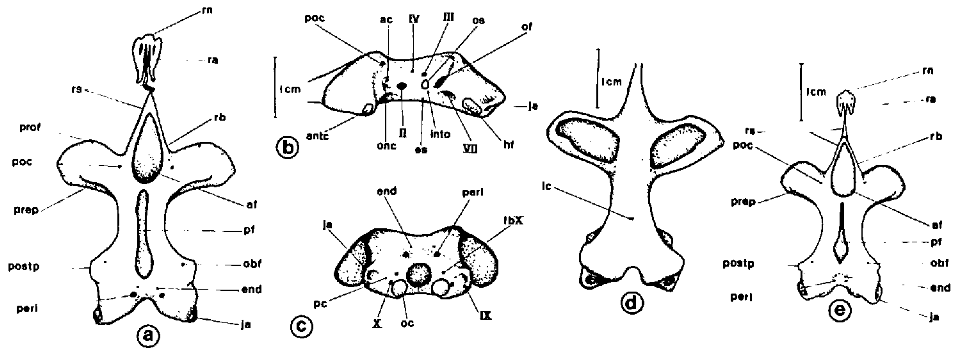


Figure 7. a, b, c, d. Neurocranium of *Breviraja colesi* MCZ 41998. a, dorsal view; b, lateral view; c, posterior view; d, ventral view. e. Neurocranium of *B. spinosa* TCWC 2728.2, dorsal view. ac—anterior cerebral vein foramen, af—anterior fontanelle, antc—antorbital condyle, end—endolymphatic foramen, es—efferent spiracular artery foramen, hf—hyomandibular facet, ic—internal carotid artery foramen, into—interorbital vein foramen, ja—jugal arch, lbX—lateralis branch of vagus nerve foramen, obf—otic branch of facial nerve foramen, oc—occipital condyle, of—orbital fissure, onc—orbitonasal canal, os—optic stalk, pc—posterior cerebral vein foramen, peri—perilymphatic foramen, pf—posterior fontanelle, poc—preorbital canal foramen, postp—postorbital process, prep—preorbital process, prof—profundus nerve foramen, ra—rostral appendix, rb—rostral base, rn—rostral node, rs—rostral shaft, II—optic nerve foramen, III—oculomotor nerve foramen, IV—trochlear nerve foramen, VII—hyomandibular branch of facial nerve foramen, IX—glossopharyngeal nerve foramen, X—vagus nerve foramen.

for anterior cerebral vein anterior and slightly dorsal to optic nerve foramen, on a line connecting preorbital canal and orbitonasal canal; trochlear nerve foramen posterior and dorsal to optic nerve foramen; oculomotor nerve foramen dorsal to optic stalk; orbital fissure on posterior aspect of orbit, anterior to foramen for hyomandibular branch of facial nerve; foramen for interorbital vein between optic stalk and orbital fissure, dorsal to foramen for efferent spiracular artery; jugal arches moderately slender; vagus nerve foramen lateral to occipital condyles, medial to foramen for glossopharyngeal nerve foramen (Fig. 7c); foramen for

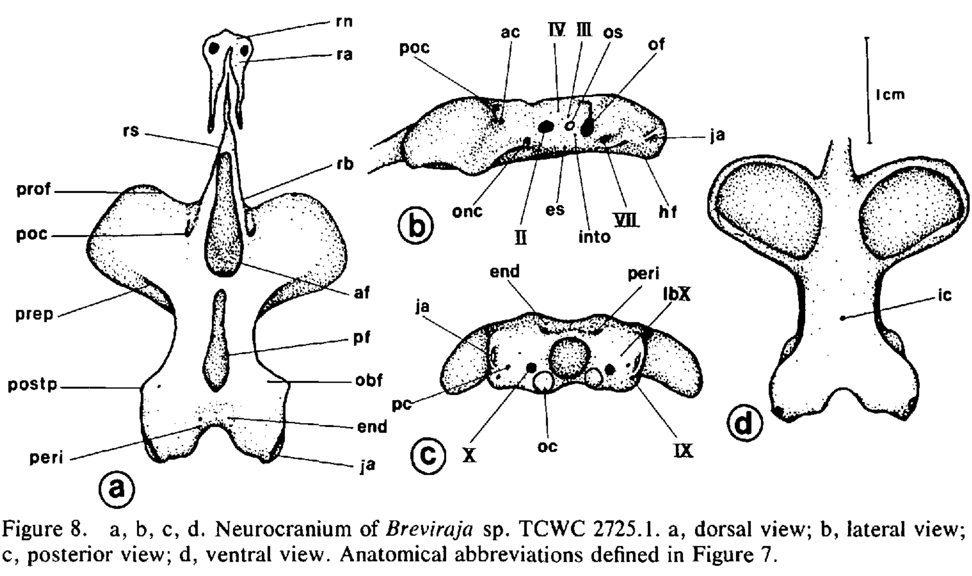


Figure 8. a, b, c, d. Neurocranium of *Breviraja* sp. TCWC 2725.1. a, dorsal view; b, lateral view; c, posterior view; d, ventral view. Anatomical abbreviations defined in Figure 7.

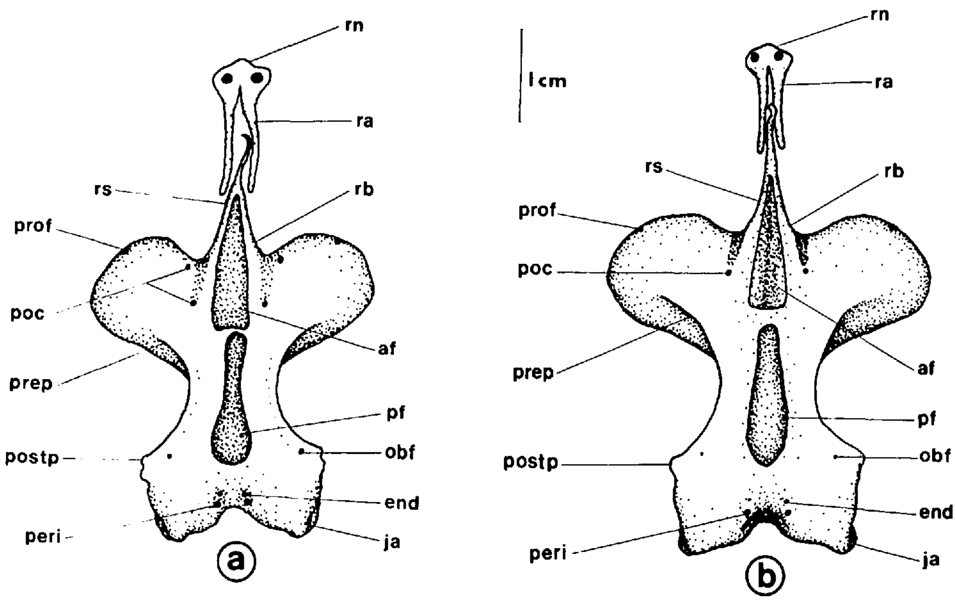


Figure 9. a. Neurocranium of *Breviraja caerulea* ISH 720/74, dorsal view. b. Neurocranium of *B. stehmanni* SAM 26638, dorsal view. Anatomical abbreviations defined in Figure 7.

lateralis branch of vagus nerve dorsal to vagus nerve foramen; basal plate moderately slender (Fig. 7d).

Neurocranium of *B. spinosa* is very similar to that of *B. colesi* except that in *B. spinosa* the rostral appendices are shorter and narrower, nasal capsules are set at about a 65° angle to long axis of neurocranium and anterior half of posterior fontanelle is narrower (Fig. 7e).

GROUP II. Neurocrania of *B. caerulea*, *B. stehmanni* and *B.* sp. greatly resemble one another and differ from those of *B. colesi* and *B. spinosa* in the following character states: rostral shaft fails to reach rostral node; distal segmented part of rostral shaft with a tapering tip; rostral appendices broad and flattened anteriorly but narrow and conical posteriorly, flanking rostral shaft; nasal capsules broad, more ovoid than rhomboid in shape; preorbital process poorly developed; anterior fontanelle narrow, shaped like an isosceles triangle; rostral base relatively narrow; jugal arches very slender; and internarial distance relatively narrow (Figs. 8, 9). *B.* sp. is distinguished from the other two species in possessing a relatively longer rostral shaft, longer rostral appendices and wider neurocranium (Fig. 8a, Table 1). *B. caerulea* is distinguished from the other two in possessing separate foramina for superficial ophthalmic branch of trigeminal nerve and superficial ophthalmic branch of facial nerve (Fig. 9a) and *B. stehmanni* is distinct in lacking a groove between preorbital process and supraorbital crest (Fig. 9b).

GROUP III. Neurocrania of *B. sinusmexicanus*, *B. sibogae*, *B. ishiyamai*, *B. cubensis*, *B. plutonia* and *B. atripinna* resemble the second morphological group in structure of rostrum and neurocranium but can be distinguished from the latter in possession of the following character states: nasal capsules possess kidney-shaped basal fenestrae and foramen for anterior cerebral vein lies posterior to line connecting preorbital canal and orbitonasal canal (Figs. 10, 11, 12). Neurocrania of the six species are very similar, however, there is much specific variation

Table 1. *Breviraja* spp. neurocranial proportions and vertebral and pectoral radial numbers, proportions expressed in percent nasobasal length are mean values (N = number of specimens measured or counted; means in parentheses)

| | *B. colesi* N = 2 | *B. spinosa* N = 1 | *B. caerulea* N = 1 | *B. stehmanni* N = 1 | *B.* sp. N = 1 | *B. sinus-mexicanus* N = 1 | *B. sibogae* N = 1 | *B. ishiyamai* N = 1 | *B. cubensis* N = 1 | *B. plutonia* N = 1 | *B. atripinna* N = 1 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nasobasal length (mm) | 300 | 218 | 300 | 325 | 246 | 321 | 273 | 372 | 229 | 269 | 275 |
| Cranial length | 170 | 171 | 158 | 166 | 183 | 169 | 178 | 200 | 169 | 149 | 182 |
| Rostral cartilage length | 69 | 71 | 58 | 66 | 80 | 71 | 82 | 95 | 68 | 53 | 81 |
| Prefontanelle length | 52 | 54 | 45 | 45 | 58 | 61 | 68 | 62 | 62 | 50 | 67 |
| Cranial width | 105 | 103 | 104 | 109 | 117 | 88 | 108 | 111 | 90 | 88 | 101 |
| Interorbital width | 29 | 29 | 29 | 29 | 33 | 26 | 31 | 29 | 26 | 26 | 25 |
| Rostral base | 31 | 27 | 17 | 17 | 15 | 16 | 22 | 14 | 13 | 09 | 15 |
| Anterior fontanelle length | 42 | 42 | 41 | 44 | 47 | 42 | 40 | 48 | 39 | 26 | 45 |
| Anterior fontanelle width | 19 | 21 | 14 | 12 | 12 | 09 | 20 | 13 | 11 | 12 | 08 |
| Posterior fontanelle length | 50 | 55 | 47 | 43 | 41 | 38 | 42 | 39 | 38 | 37 | 40 |
| Posterior fontanelle width | 09 | 09 | 12 | 11 | 10 | 11 | 13 | 12 | 11 | 11 | 12 |
| Rostral appendix length | 37 | 30 | 43 | 39 | 48 | 62 | 59 | 90 | 48 | 36 | 56 |
| Rostral appendix width | 21 | 22 | 15 | 16 | 20 | 18 | 15 | 12 | 10 | 09 | 13 |
| Rostral cleft length | 16 | 21 | 32 | 28 | 41 | 49 | 48 | 83 | 39 | 30 | 48 |
| Cranial height | 28 | 30 | 25 | 24 | 23 | 21 | 23 | 22 | 19 | 20 | 21 |
| Width across otic capsules | 54 | 58 | 58 | 56 | 60 | 51 | 59 | 52 | 50 | 51 | 51 |
| Least width of basal plate | 29 | 27 | 28 | 25 | 30 | 23 | 28 | 26 | 24 | 25 | 23 |
| Greatest width of nasal capsule | 38 | 35 | 45 | 46 | 49 | 37 | 44 | 49 | 40 | 40 | 41 |
| Internarial width | 22 | 21 | 10 | 11 | 15 | 13 | 18 | 13 | 09 | 07 | 12 |
| | N = 5 | N = 5 | N = 13* | N = 15† | N = 2 | N = 10 | N = 2‡ | N = 2 | N = 3 | N = 5 | N = 5 |
| Trunk vertebrae | 26–31 (29) | 28–29 (29) | 23–26 (25) | 24–26 (26) | 25–27 (26) | 20–23 (22) | 24 (24) | 24–25 (25) | 22–23 (23) | 21–24 (23) | 24–25 (25) |
| Predorsal tail vertebrae | 72–79 (77) | 71–73 (72) | 69–74 (72) | 65–74 (71) | 67–71 (69) | 70–74 (73) | 66–71 (69) | 72–74 (73) | 64–70 (67) | 65–75 (69) | 65–76 (71) |
| Total vertebrae | 102–109 (106) | 99–102 (101) | 92–100 (97) | 91–98 (97) | 94–96 (95) | 93–97 (95) | 90–95 (93) | 97–98 (98) | 86–93 (90) | 88–97 (90) | 94–100 (97) |
| Pectoral radials | 70–75 (72) | 66–68 (66) | 62–68 (66) | 60–61 (61)§ | 58–62 (60) | 57–61 (59) | 61–66 (63) | 61–62 (62) | 58–59 (58) | 56–59 (57) | 62–65 (64) |

* Data from Stehmann (1976b).
† Data from Hulley (1972b).
‡ Data from Stehmann (1976a).
§ Number of pectoral radials was not given by Hulley (1972b), counts were made on two specimens borrowed from SAM.

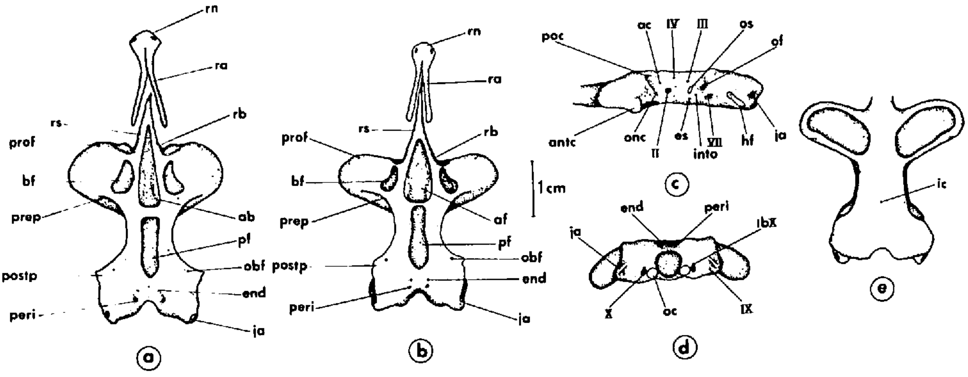


Figure 10. a. Neurocranium of *Breviraja sinusmexicanus* TCWC 2696.1, dorsal view. b, c, d, e. Neurocranium of *B. sibogae* ZMA 112.640. b, dorsal view; c, lateral view; d, posterior view; e, ventral view. bf—basal fenestra, all other anatomical abbreviations given in Figure 7.

and several of the species share derived character states which suggest sister group relationships. *B. sinusmexicanus*, *B. sibogae* and *B. ishiyamai* are distinguished by possession of nasal capsules which bulge only slightly into precerebral space (a plesiomorphic character state). *B. sinusmexicanus* and *B. sibogae* possess a cartilaginous ridge along anteroventral aspect of the nasal capsules which forms a step-like structure running from rostral base to leading edge of nasal capsule (Fig. 10). *B. ishiyamai* has longest rostral cartilage and rostral appendices (Fig. 12, Table 1). In *B. cubensis*, *B. plutonia* and *B. atripinna* nasal capsules distinctly bulge into precerebral space (Figs. 11, 12). Within the latter three species, *B. cubensis* and *B. plutonia* have a narrower internarial distance and more medially bulging nasal capsules, *B. atripinna* has the most laterally expanded nasal capsules and *B. cubensis* and *B. atripinna* have more similar shaped anterior fontanelles.

Rostrum of *B. yucatanensis* is distinguished from those of all of the above species in that rostral shaft is slender but stouter than in other species, tapers to its junction with rostral node and is unsegmented. As in *B. colesi* and *B. spinosa*, rostral appendices are moderately short, laterally expanded and flattened over

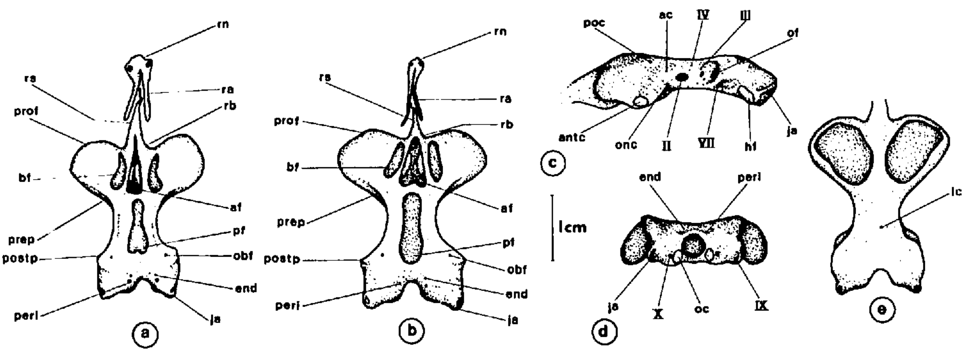


Figure 11. a. Neurocranium of *Breviraja cubensis* MCZ 41928, dorsal view. b, c, d, e. Neurocranium of *B. plutonia* MCZ 41170. b, dorsal view; c, lateral view; d, posterior view; e, ventral view. Anatomical abbreviations defined in Figures 7 and 10.

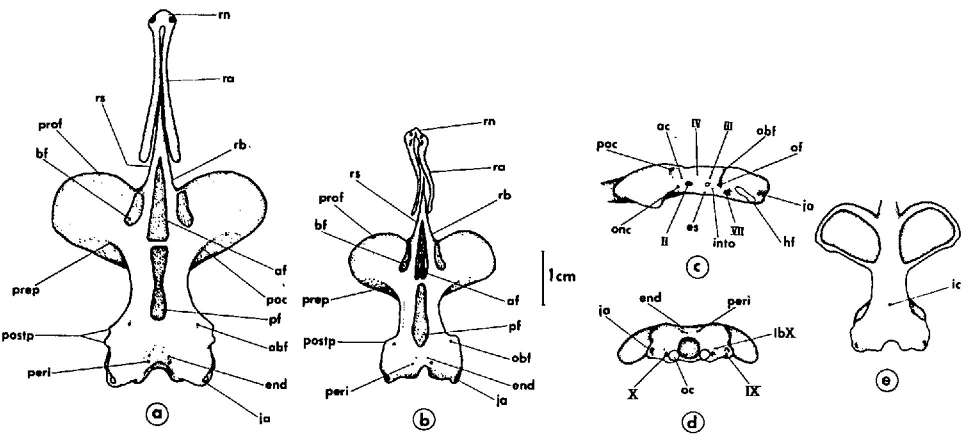


Figure 12. a. Neurocranium of *Breviraja ishiyamai* MCZ 40665, dorsal view. b, c, d, e. Neurocranium of *B. atripinna* MCZ 41828. b, dorsal view; c, lateral view; d, posterior view; e, ventral view. Anatomical abbreviations defined in Figures 7 and 10.

their entire length, however, unlike all of the other species of *Breviraja*, pectoral radials fall distinctly short of rostral node.

*Scapulocoracoids*.—The scapulocoracoids of the 11 species of *Breviraja* examined are of the same basic design. All lack an anterior bridge and are relatively short with mesocondyle equidistant or only slightly posterior to midlength of scapulocoracoid (Table 2). *B. spinosa* has the least derived scapulocoracoid in that the lateral face is high and short and fenestrae are little expanded (Figs. 13, 14) (McEachran and Compagno, 1979; Compagno and McEachran, in prep.). That of *B. colesi* is more elongated, almost rectangular in outline, with fenestrae expanded. Scapulocoracoids of *B. stehmanni, B. caerulea* and *B.* sp. are very similar to each other in that the dorsal margin, posterior to suprascapula, is concave with rear corner elevated and posterodorsal margin slanting diagonally towards metacondyle. Those of *B. sinusmexicanus, B. sibogae, B. ishiyamai* and *B. atripinna* are similar in that they are moderately elongated with multiple postventral foramina. Postdorsal margin, posterior to rear corner, is gently sloped in *B. sinusmexicanus* and *B. sibogae* but abruptly sloped in *B. ishiyamai* and *B.*

Table 2. *Breviraja* spp. scapulocoracoid proportions expressed in percent greatest length (N = number of specimens measured)

| | *B. colesi* N = 2 | *B. spinosa* N = 1 | *B. caerulea* N = 1 | *B. stehmanni* N = 1 | *B.* sp. N = 1 | *B. sinusmexicanus* N = 1 | *B. sibogae* N = 1 | *B. ishiyamai* N = 1 | *B. cubensis* N = 1 | *B. plutonia* N = 1 | *B. atripinna* N = 1 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Greatest length (mm) | 148 | 95 | 129 | 156 | 114 | 155 | 156 | 209 | 95 | 94 | 144 |
| Greatest height | 89 | 143 | 84 | 97 | 75 | 79 | 67 | 73 | 65 | 100 | 63 |
| Premesocondyle | 47 | 44 | 51 | 45 | 44 | 47 | 42 | 38 | 47 | 47 | 42 |
| Postmesocondyle | 53 | 56 | 49 | 55 | 56 | 54 | 58 | 62 | 53 | 53 | 58 |
| Postdorsal fenestra length | 17 | 09 | 12 | 13 | 13 | 19 | 29 | 30 | 10 | 01 | 32 |
| Postdorsal fenestra height | 14 | 09 | 12 | 12 | 10 | 16 | 22 | 22 | 07 | 01 | 22 |
| Anterior fenestra length | 16 | 13 | 19 | 18 | 14 | 14 | 22 | 16 | 17 | 17 | 17 |
| Anterior fenestra height | 17 | 17 | 22 | 22 | 26 | 23 | 28 | 31 | 21 | 26 | 27 |
| Height of rear corner | 72 | 82 | 73 | 78 | 66 | 61 | 53 | 52 | 72 | 90 | 51 |

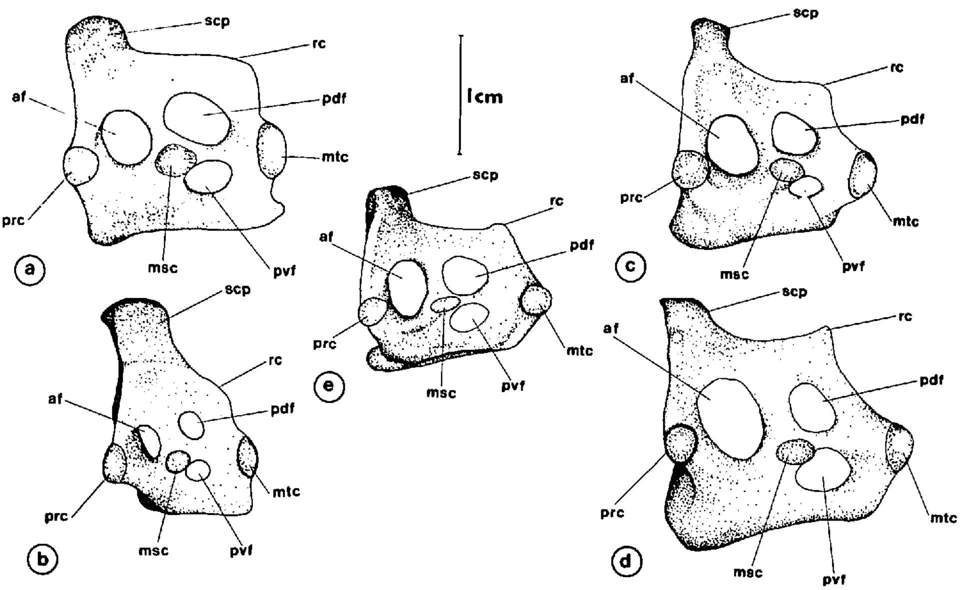


Figure 13. Lateral view of scapulocoracoid. a, *Breviraja colesi* MCZ 41998; b, *B. spinosa* TCWC 2728.2; c, *B.* sp. TCWC 2725.1; d, *B. caerulea* ISH 720/74; e, *B. stehmanni* SAM 26638. af—anterior fontanelle, msc—mesocondyle, mtc—metacondyle, pdf—postdorsal fenestra, prc—procondyle, pvf—postventral foramina, rc—rear corner, scp—scapular process.

*atripinna*. Postdorsal fenestra is elongated in *B. sibogae, B. ishiyamai* and *B. atripinna*. Scapulocoracoids of *B. cubensis* and *B. plutonia* resemble those of *B. caerulea, B. stehmanni* and *B.* sp. in shape of the rear corner and postdorsal margin and in possessing only one postventral foramen. Scapulocoracoid of *B. plutonia* is considerably shorter than those of the other species.

*Number of Vertebrae*.—Number of predorsal caudal vertebrae of the 12 species of *Breviraja* suggested almost the same grouping of species as the above character complexes (Table 1). *B. colesi, B. spinosa* and *B. yucatanensis* have the greatest number of trunk vertebrae ($\bar{x}$ = 29, 29, 27 respectively), *B. stehmanni, B. caerulea, B. atripinna* and *B.* sp. made up the second subgroup ($\bar{x}$ = 25–26) and *B. plutonia, B. cubensis, B. sinusmexicanus, B. sibogae* and *B. ishiyamai* comprised the third subgroup ($\bar{x}$ = 22–24).

## Discussion

*Interrelationships within* Breviraja.—Character complexes examined in this study indicate that *Breviraja* consists of three morphological groups. Group I, including *B. colesi* and *B. spinosa* is distinguished by its possession of oronasal pits, strap-shaped dorsal terminal 1 cartilage; dorsal terminal 2 with distal extension forming promontory; dorsal terminal 3 which proximomedially lies on inner surface of dorsal terminal 2 forming hook; J-shaped ventral terminal with an anterior notch and distal medial process which wraps around axial; slender and segmented rostral shaft which joins rostral node at tip of snout; rostral appendices with wide and flat posterior extremities; moderately broad rostral base; relatively broad anterior fontanelle; well developed preorbital processes; moderately broad internarial distance; and high number of trunk vertebrae. Group II, including *B. steh-*

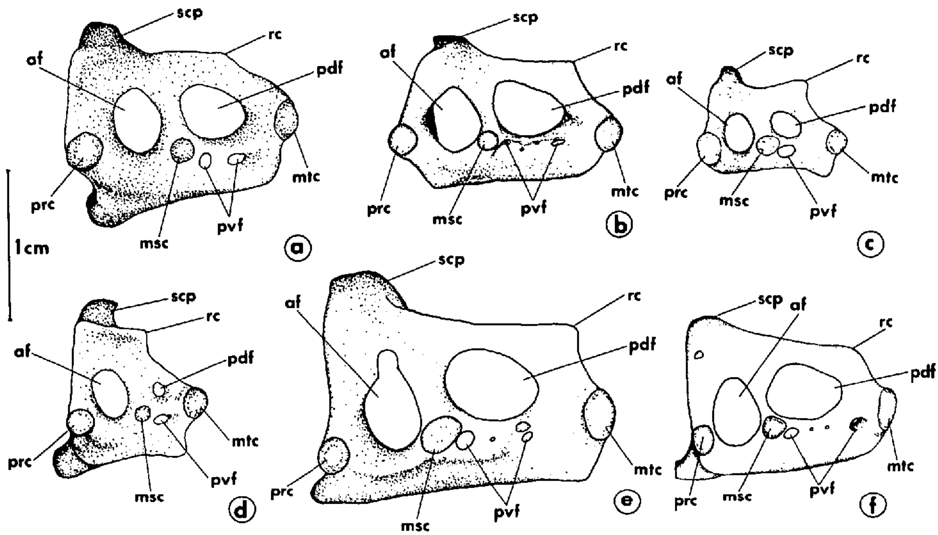

Figure 14. Lateral view of scapulocoracoid. a, *Breviraja sinusmexicanus* TCWC 2696.1; b, *B. sibogae* ZMA 112.640; c, *B. cubensis* MCZ 41928; d, *B. plutonia* MCZ 41170; e, *B. ishiyamai* MCZ 40665; f, *B. atripinna* MCZ 41828. Anatomical abbreviations defined in Figure 13.

*manni, B. caerulea* and *B.* sp., is distinguished by its lack of oronasal pits; dorsal terminal 1 cartilage with proximal extension, proximally located sentinel and spike; ventral terminal with an anterior notch but without expansion of inner distal margin to wrap around axial; incomplete rostral shaft; conical rostral appendices; relatively narrow rostral base; relatively narrow anterior fontanelle; poorly developed preorbital processes; slender jugal arches; relatively narrow internarial distance; scapulocoracoid with notch-like rear corner; and low number of trunk vertebrae. Interrelationships within the group are uncertain since no two of the species share a derived character state and probably will remain so until a mature male specimen of *B.* sp. with a fully developed clasper is available for study.

Group III, including *B. sinusmexicanus, B. sibogae, B. ishiyamai, B. cubensis, B. plutonia* and *B. atripinna* is distinguished by its possession of an oronasal pit; lack of dorsal terminal 1 cartilage; distally located sentinel and spike; check-shaped ventral terminal which lacks an anterior notch; dorsal marginal which enters inner dorsal surface of glans; incomplete rostral shaft; conical rostral appendices; very narrow rostral base; narrow anterior fontanelle (all species except *B. sibogae*); poorly developed preorbital processes; slender jugal arches; nasal capsules with basal fenestrae; posterior positioned foramen for anterior cerebral vein; and low number of trunk vertebrae. Within this group interrelationships are less certain because of the large amount of specific variation and paucity of synapomorphies shared by pairs of species. However, the unique step-like process on the anteroventral aspect of the nasal capsules of *B. sinusmexicanus* and *B. sibogae* suggest that they form a sister group. The other four species share a unique character state for rajoids, tapering proximal extension of the accessory terminal 1 cartilage lying on dorsal surface of ventral marginal cartilage, suggesting that these species represent the apomorphic sister group of *B. sinusmexicanus* and *B. sibogae*. *B. cubensis, B. plutonia* and *B. atripinna* share one apomorphic character state, bulging of nasal capsules into the precerebral space,

suggesting that they represent the apomorphic sister group of *B. ishiyamai*. *B. cubensis* and *B. plutonia* possess the narrowest internarial distance and fewest number of vertebrae and pectoral radials, suggesting that they are sister species and the plesiomorphic sister group of *B. atripinna* which possesses the unique finger-like projection of the dorsal marginal cartilage.

Based on the structure of the rostrum, *B. yucatenensis* more closely resembles the *Raja* subgenera *Leucoraja, Rajella* and *Malacoraja,* especially *Raja garmani,* a species derived from or a member of *Leucoraja* (McEachran and Martin, 1978) than it does *Breviraja*. In the above *Raja* taxa the rostral shaft is very slender and uncalcified near its junction with the appendices, and the rostral appendices are free of the rostral shaft over most of their length. Also in the above *Raja* taxa, as in *B. yucatanensis,* the pectoral radials fall distinctly short of the rostral node. Thus *B. yucatanensis* is reallocated to the genus *Raja* and is considered a sister species of *Raja garmani* which it resembles in morphology, coloration and structure of the rostrum and neurocranium. It is distinguished from *R. garmani* by its number of trunk vertebrae (27 vs 23–26, $\bar{x}$ = 24.4), predorsal tail vertebrae (68 vs 58–63, $\bar{x}$ = 60.0) and pectoral radials (69 vs 64–65, $\bar{x}$ = 64.5). Counts for *R. garmani* were taken from values listed by McEachran (1977) for the Caribbean subspecies *R. garmani caribbaea*.

*Relationships of* Breviraja *with other Rajoid Taxa*.—Stehmann and Hulley have considered *Breviraja* a monophyletic taxon and a primitive derivative of the family Rajidae because of its high number of predorsal caudal vertebrae and primitive characteristics of its clasper, i.e. retention of dermal denticles, axial cartilage with a pointed tip and Z-shaped lateral projection of the accessory terminal 1 cartilage (Hulley, 1972b). Hulley (1972b) further stated that *Breviraja* was a very early split off the *Raja* subgenera *Dipturus/Amblyraja/Leucoraja/Rajella* line while Hulley and Stehmann (1977) and Stehmann (1977) considered *Raja* (*Malacoraja*) a connecting link between *Breviraja* and the evolutionary line *Dipturus/Rajella/Amblyraja/Leucoraja* because of the similarities of the claspers and neurocrania of *Breviraja caerulea, B. stehmanni, Raja* (*Malacoraja*) *kreffti* and *R.* (*M.*) *spinacidermis*.

It is difficult to determine if the clasper of *Breviraja* is primitive or derived because claspers of rajoids have not been compared in detail with those of other elasmobranchs and thus it is difficult to determine the polarity of character states. Also the claspers of rajoids are extremely variable and it is very possible that several or many evolutionary pathways in clasper structure have evolved. Although a high number of predorsal caudal vertebrae may be primitive for Rajidae (Ishiyama, 1958), it is possible, considering the great species diversity within Rajoidei, that the trend for reduction in tail vertebrae was reversed in *Breviraja*.

*Breviraja* possesses a number of character states which are considered derived for Rajoidei and specializations of the rostrum can be considered derived over that in the genus *Raja*. The 11 species of *Breviraja* treated herein possess some or all of the following character states which McEachran and Compagno (1979) considered derived within Rajoidei: internasal septum extremely narrow, with inner walls of nasal capsules bulging medially; basal plate extremely narrow, especially at orbits; jugal arches very slender; roof of each nasal capsule with a basal fenestra; presence of a rostral process; caudal fin with a ventral lobe which is discontinuous with dorsal lobe; nasal capsules greatly expanded anterolaterally; and supraorbital crests deeply incised. None of these character states are unique to *Breviraja,* but possession of them suggest that *Breviraja* is a derived rather than a primitive taxon.

Previous authors have stated that the rostral shaft of *Breviraja* is a very slender

bar which joins the rostral appendices at the tip of the snout and, posterior to this junction, the appendices are free of the rostral shaft (Ishiyama and Hubbs, 1968; Hulley, 1972b; Stehmann, 1976b). Ishiyama (1958), Stehmann (1970), and Hulley (1970; 1972a) have also stated that the rostral appendices in the genus *Raja* are fused to the rostral shaft over their entire length. However, in *Breviraja* the rostral shaft joins the appendices at the tip of the snout in only two of the 11 species (*B. colesi* and *B. spinosa*) investigated herein. Also, the rostral shaft in the *Raja* subgenera *Leucoraja, Rajella* and *Malacoraja* is very similar to those of *B. colesi* and *B. spinosa* except that it is slightly stouter, tapered over its entire length and lacks segmentation. Thus the condition of the rostrum in *Breviraja* appears to be a derived state over that in *Leucoraja, Rajella* and *Malacoraja*. In *Breviraja* the rostral shaft has become more slender and segmented (*B. colesi* and *B. spinosa*) or terminates proximal to the rostral node (9 other species). Also the rostral appendices in all *Breviraja* species except *B. colesi* and *B. spinosa* are conical over most of their length, a derived state unique to them and several other rajoids, i.e. *Gurgesiella, "Raja" waitei, Bathyraja asperula* and *B. spinifera* (McEachran and Compagno, 1979; Compagno and McEachran, in preparation).

Comparison of the claspers, neurocrania, scapulocoracoids and vertebral numbers of the three *Breviraja* morphological groups with those of other rajoid taxa reveals (Fig. 15): 1. Group I (*B. colesi* and *B. spinosa*) most closely resembles *Raja* (*Leucoraja*). 2. Group II (*B. caerulea, B. stehmanni* and *B.* sp.) most closely resembles *Raja* (*Malacoraja*). 3. Group III (*B. sinusmexicanus, B. sibogae, B. ishiyamai, B. cubensis, B. plutonia* and *B. atripinna* closely resembles both group II and *Gurgesiella* and is more derived than the former and less derived than the latter taxon. These findings suggest either that *Breviraja* is monophyletic but that considerable parallel evolution has occurred between *Breviraja* species and other rajoid taxa or that *Breviraja* is paraphyletic and that parallel evolution has occurred between the *Raja* subgenera *Leucoraja* and *Malacoraja*, the postulated ancestral taxa of *Breviraja*.

Based on shared derived characters (Fig. 15) the second hypothesis, that *Breviraja* is paraphyletic, is the more parsimonious. The second hypothesis requires 9 cases of parallel evolution of character states while the first hypothesis requires 15. (In counting the number of character states derived in parallel, it was assumed that absence of oronasal pits, tapering proximal extension of accessory terminal 1 and distal segmented part of rostral shaft in *Gurgesiella*; relatively wide anterior fontanelle in *B. sibogae*; short, high scapulocoracoid in *B. plutonia*; and relatively high number of trunk vertebrae in *B. atripinna* represent evolutionary reversals from the apomorphic to the plesiomorphic state. However, rejection of any or all of these assumptions would not corroborate the first hypothesis over the second.) Group I shares only three apomorphic character states with groups II and/or III and these are judged to be of minor importance, i.e. presence of oronasal pits, loss of a terminal bridge in the dorsal lobe of the clasper and segmentation of the rostral shaft. Oronasal pits and segmented rostral shafts have apparently evolved several times within Rajoidei. Oronasal pits also occur in "*Raja*" (*Rioraja*) *agassizi*, "*Raja*" *waitei*, *Raja* (*Rostroraja*) *alba* and *Pseudoraja fischeri* and segmented rostra also occur in *Rhinoraja* (Ishiyama, 1958), some species of *Bathyraja*, and in "*Raja*" *waitei, Psammobatis, Sympterygia* (Compagno and McEachran, in prep.) and *Arhynchobatis asperrimus* (Garrick, 1954). Loss of character state, such as the terminal bridge, offers little information in determining phylogenies because there is no way of determining whether the state resulted from a single change or by two or more independent processes between the two taxa (Hecht and Edwards, 1977).

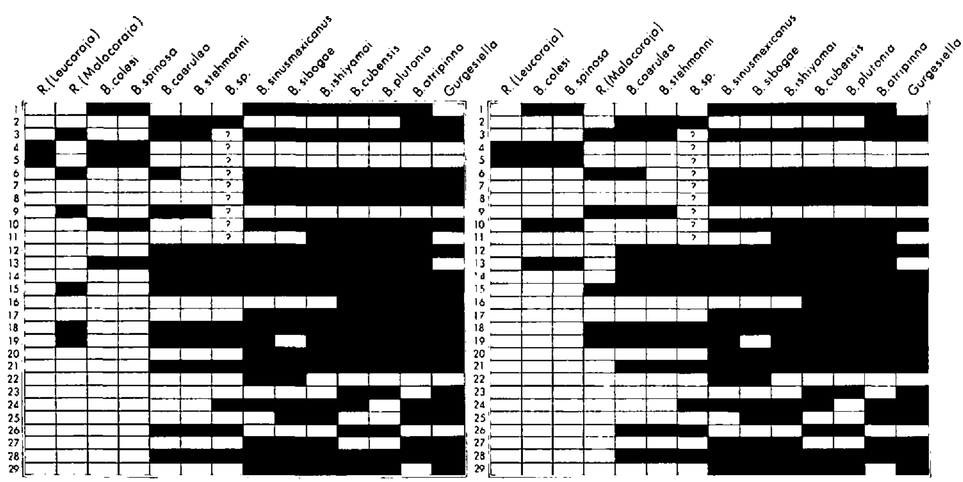

Figure 15. Synapomorphic character states shared among *Raja* subgenera *Leucoraja* and *Malacoraja*, *Breviraja* species and *Gurgesiella*. Taxa listed according to current classification of genera, assuming that *Breviraja* is monophyletic (left) and according to reclassification of genera, assuming that *Breviraja* is paraphyletic (right). enclosed rectangles = apomorphic state. open rectangles = plesiomorphic state. ? = character state unknown. Numbers on left vertical margin represent characters: 1 = oronasal pits (apomorphic character state: present), 2 = ventral caudal lobe (present), 3 = pseudosiphon (absent), 4 = dorsal terminal 3 cartilage with proximal extension overlapping medial surface of dorsal terminal 2 cartilage (present), 5 = promontory (present), 6 = flag (present), 7 = dorsal terminal 1 cartilage (absent), 8 = ventral terminal cartilage with anterior notch (absent), 9 = accessory terminal cartilages (proximally located), 10 = terminal bridge (absent), 11 = accessory terminal 1 cartilage with tapering proximal extension along medial surface of ventral marginal cartilage (present), 12 = rostral shaft (incomplete), 13 = rostral shaft (segmented), 14 = rostral appendices (conical), 15 = nasal capsules (ovoid in shape), 16 = nasal capsules (bulging medially), 17 = basal fenestra on nasal capsules (present), 18 = preorbital process (poorly developed), 19 = anterior fontanelle (narrow), 20 = foramen for anterior cerebral vein (posterior to line connecting preorbital canal and orbitonasal canal), 21 = jugal arches (very slender or absent), 22 = step-like process on anteroventral aspect of nasal capsules (present), 23 = internarial width (very narrow), 24 = height of scapulocoracoid (less than 80% of length), 25 = postdorsal fenestra of scapulocoracoid (elongated), 26 = rear corner of scapulocoracoid (elevated), 27 = number of postventral foramina (multiple), 28 = trunk vertebrae (less than 28), 29 = trunk vertebrae (less than 25).

*Leucoraja* and group I share two apomorphic character states which are unique for Rajoidei, i.e., presence of a promontory in the dorsal lobe of the glans and presence of a free proximal extension of the dorsal terminal 3 lying on medial surface of dorsal terminal 2.

*Malacoraja* shares six apomorphic character states with group II and five with groups II and III, and four of these are judged to be of phylogenetic importance, i.e., proximal position of the sentinel and spike, ovoid shape of the nasal capsules, poorly developed preorbital processes and narrow anterior fontanelles. These character states are thought to be unique to *Malacoraja* and groups II and III or to *Malacoraja*, groups II and III, *Gurgesiella* and *Pseudoraja* (McEachran and Compagno, 1979).

The hypothesis of phylogenetic relationship seemed to correlate well with similarity of character complexes examined and those morphoclines that were investigated. The claspers of group I are very similar but either more simplified or specialized than those of *Leucoraja* and may be the result of simplification or embellishment of the *Leucoraja* type clasper. Both groups possess pseudosiphons which are formed in part or in total by the dorsal dilatator muscles, dorsal mar-

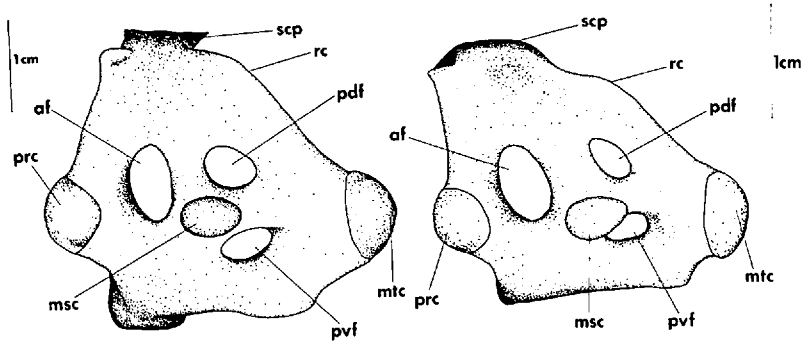


Figure 16. Lateral view of scapulocoracoid. Left, *Raja* (*Leucoraja*) *erinacea* TCWC 2742.1; Right, *R.* (*Malacoraja*) *senta* VIMS 1538. Anatomical abbreviations defined in Figure 13.

ginal cartilages with truncate distal margins and similarly shaped dorsal terminal 1, accessory terminal 1 and accessory terminal 2 cartilages (Stehmann, 1970; Hulley, 1972b; McEachran and Martin, 1978). Unlike most *Leucoraja* species group I possesses three rather than four dorsal terminal cartilages, and lacks a spur and a terminal bridge. However, *Raja* (*Leucoraja*) *erinacea* and *R.* (*L.*) *ocellata* likewise possess three dorsal terminals and lack a spur and terminal bridge (McEachran and Martin, 1978). The two *Leucoraja* species differ from group I in that the free proximal extension of the dorsal terminal 3 is not recurved towards the tip of the clasper. The neurocrania of group I is more similar to that of *Leucoraja* than to those of *Malacoraja* and groups II or III in that the rostral base, anterior fontanelle and internarial distance are relatively broad, nasal capsules are rhomboid in shape and preorbital processes and jugal arches are moderately well developed (McEachran and Martin, 1978). The rostral appendices of the two groups are similar but the rostral shaft in *Leucoraja* is stouter and unsegmented. The scapulocoracoid of group I resembles that of *Leucoraja* in being

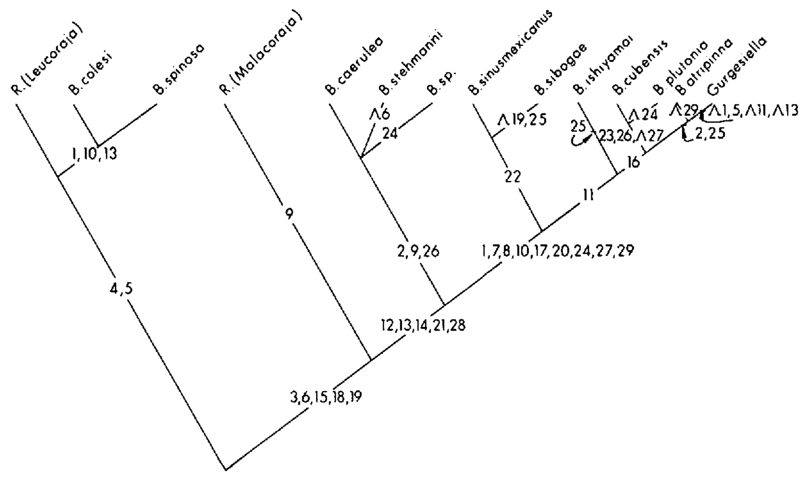


Figure 17. A phylogeny of *Breviraja* and related taxa. Numbers correspond to synapomorphic character states listed in Figure 15.

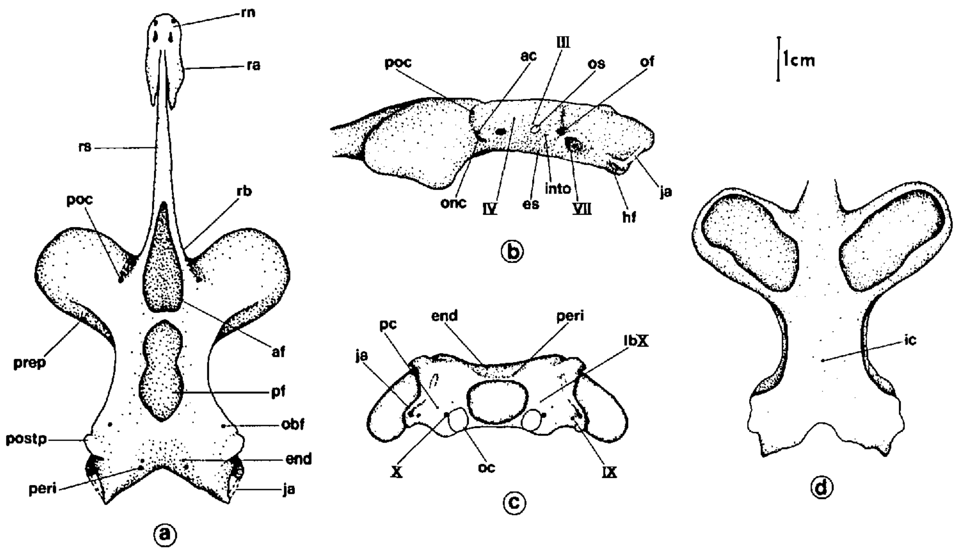


Figure 18. Neurocranium of *Raja* (*Malacoraja*) *senta* VIMS 1538. a, dorsal view; b, lateral view; c, posterior view; d, ventral view. Anatomical abbreviations defined in Figure 7.

little expanded horizontally and in possessing a single postventral foramen (Fig. 16 Left).

Group I is more similar to *Leucoraja* than to the other two groups or *Malacoraja* in number of trunk and predorsal tail vertebrae and in squamation. *Leucoraja* possesses from 23 to 37 trunk vertebrae (all but two species have 30 or more) and 50 to 81 predorsal tail vertebrae (all but two species have more than 62) (McEachran and Martin, 1978). Group I and *Leucoraja* possess a distinct triangular patch of thorns over the scapular and nuchal regions and a wide band of thorns over the mid-dorsal disc and tail, and the thorns of the dorsolateral row are of equal or larger size than those of the mid-row (Bigelow and Schroeder, 1953; McEachran and Musick, 1973; McEachran and Martin, 1978). The two other groups and *Malacoraja* lack a distinct triangular patch of thorns and the broad band of thorns along the midline of the disc and tail (except *B. sinusmexicanus*) (Bigelow and Schroeder, 1953; Hulley, 1972b; Stehmann, 1976b; 1977; Hulley and Stehmann, 1977).

*Malacoraja* and groups II and III appear to form a morphocline with *Malacoraja* the plesiomorphic taxon and *B. atripinna* the autapomorphic taxon (Fig. 17). The claspers of *Malacoraja* and group II are very similar and based on them alone the two taxa could be considered sister groups. However, this interpretation would require the independent development of incomplete, segmented rostral shafts; high number of predorsal tail vertebrae; and conical rostral appendices in groups II and III. In both *Malacoraja* and group II sentinel and spike are medially located, dorsal terminal 1 and ventral terminal are joined ventrally and the cartilages are similarly shaped, except that in group II the dorsal terminal 1 possesses a proximal extension (Hulley, 1972b; Stehmann, 1976b; 1977; Hulley and Stehmann, 1977). The neurocranium of *Malacoraja,* like those of groups II and III, is specialized for rajoids in that the rostral base, anterior fontanelle and internarial distance are narrow, the preorbital processes are poorly developed and nasal capsules are greatly expanded laterally and ovoid in shape (Fig. 18; Hulley and

Stehmann, 1977; Stehmann, 1977). Although the rostral shaft in *Malacoraja* is slender and uncalcified distally, it is not segmented and incomplete as in groups II and III. Also the rostral appendices in *Malacoraja*, although largely free of the rostral shaft, are not conical as in groups II and III. The scapulocoracoid of *Malacoraja* is similar to that of group II except that it lacks a distinctly elevated rear corner (Fig. 16b). *Malacoraja* has similar number of trunk vertebrae (24 to 29 vs 23 to 27) but slightly fewer predorsal caudal vertebrae (60 to 69 vs 65 to 74) than group II. *Malacoraja* and group II have similar squamation; thorns are reduced to several nuchal and scapular thorns and there is a single midline series of thorns from the scapular region to the first dorsal fin. The dorsal surface and dorsal-lateral surface of tail are more or less uniformly covered with denticles.

Groups II and III share nine synapomorphies, four of which are judged to be of phylogenetic importance, i.e. incomplete rostral shaft, segmented rostral shaft, conical rostral appendices and less than 28 trunk vertebrae, and group III possesses a number of specializations of the clasper and neurocranium which suggest that it was derived from group II. Group III has lost dorsal terminal 1 and developed a simplified ventral terminal cartilage which lacks an anterior notch. The neurocrania of group III is more derived than that of group II in possessing basal fenestra on the nasal capsule and posteriorly positioned foramina for the anterior cerebral vein. Also all species of group III except *B. atripinna* have further reduced the number of trunk vertebrae to less than 25.

*Gurgesiella* shares a large number of derived character states with groups II and III and has continued the morphocline established in *Malacoraja*. Claspers, neurocrania and scapulocoracoids of *Gurgesiella* are of the same basic design but, in many respects, more derived than those of group III (McEachran and Compagno, 1979). Clasper cartilages are similarly shaped except that in *Gurgesiella* dorsal marginal has a longer distolateral process that forms the pseudorhipidion, a dorsal terminal 3 with a crenate margin which fails to join the axial, a ventral terminal with an expanded proximal section and a distomedial process that is perpendicular to axis of clasper (incorrectly termed an anterior notch by McEachran and Compagno, 1979) and an accessory terminal 1 with a long proximal lateral arm which forms part of the margin of the ventral lobe. The rostral shaft terminates prior to the rostral node but lacks a segment; perhaps the section distal to the segment in *Breviraja* has been lost. The nasal capsules bulge more extensively than in group III and the jugal arches are lacking. The scapulocoracoid is more anteroventrally expanded than in group III. The number of trunk vertebrae ($\bar{x}$ = 22.5 and 23.0) and squamation correspond to the values in group III. As in *Malacoraja* and groups II and III, *Gurgesiella* is sparcely covered with thorns (thorns occur only along the dorsal midline of tail) and is uniformly covered with denticles.

*Gurgesiella* most closely resembles *B. cubensis*, *B. plutonia* and *B. atripinna* and presumably could share a common ancestor with any of these species. However, *B. atripinna* shares two derived character states with *Gurgesiella*: scapulocoracoid with multiple postventral foramina and tail with a hypochordal lobe; and one with *B. cubensis* and *B. plutonia*: very narrow internarial distance; thus it is considered the sister species to *Gurgesiella*.

McEachran and Compagno (1979) stated that *Gurgesiella* and *Pseudoraja* form a sister group sharing a number of derived character states and that both are members of the family Pseudorajidae. However, it is now apparent that several of these character states including narrowness of the internasal septum (also occurring in *Breviraja cubensis*, *B. plutonia* and *B. atripinna*), narrowness of the basal plate (also occurring in *Breviraja* groups II and III) and slenderness of the

jugal arches (also occurring in *Breviraja* groups II and III) are not unique to *Gurgesiella* and *Pseudoraja*. *Pseudoraja* and *Gurgesiella* thus share two synapomorphies; anterior pelvic lobes greatly expanded laterally, with posterior margins more or less straight, and nostrils greatly elongated anteroposteriorly. Considering the difference between the genera in shape of the scapulocoracoid (McEachran and Compagno, 1979) it is best to reserve judgment on their relationship until claspers of *Pseudoraja* are available for study. In fact the status and taxonomic composition of all the families of Rajoidei (Rajidae, Arhynchobatidae, Pseudorajidae, Anacanthobatidae and Crurirajidae) cannot be determined until the interrelationships within all of the genera and subgenera have been worked out.

The interrelationships among the three morphological groups in *Breviraja* and their relationships with the *Raja* subgenera *Leucoraja* and *Malacoraja* and the genus *Gurgesiella* necessitate the following nomenclatorial changes within Rajoidei: 1. *Breviraja* is restricted to group I (*B. colesi*, type species of *Breviraja* and *B. spinosa*). 2. The genus *Neoraja* is erected for *Breviraja* groups II and III. 3. The subgenera *Neoraja* and *Fenestraja* are proposed for groups II and III. These changes are necessary because group I is the apomorphic sister group of *R.* (*Leucoraja*) and groups II and III and *Gurgesiella* constitute the apomorphic sister group of *R.* (*Malacoraja*). Classification of *B. mamillidens* will remain uncertain until specimens are available for study, however, based on the illustration by Alcock (1889) the species can tentatively be placed in *Neoraja*, based on external shape and spination. The snout, tail and anterior pelvic lobes are relatively long and midbelt thorns are limited to a single row as in *Neoraja*. The status of *R.* (*Leucoraja*), *R.* (*Malacoraja*) and *Gurgesiella* will be dealt with later along with all genera and subgenera of Rajoidei (Compagno and McEachran, in prep.).

### *Breviraja* Bigelow and Schroeder, 1948

*Type Species.*—*Breviraja colesi* Bigelow and Schroeder, 1948, by original designation.

*Description.*—Rajoids with thorns along inner margin of orbits, forming a triangular patch over scapular and nuchal region, along midline of disc in either one incomplete row or three to five complete but irregular rows and dorsal surface of tail with five to seven irregular rows; dorsal surface more or less evenly covered with denticles; shape of disc oval, snout obtuse, outer and posterior margins broadly rounded; pelvic fins deeply incised, anterior lobe short, narrow and bluntly tipped; tail relatively broad proximally, moderately long (about 60% or less total length), with two small dorsal fins, with a dorsal caudal lobe but without a ventral caudal lobe; with oronasal pits; dorsal surface plain colored or mottled with irregular spots and blotches, ventral surface plain whitish to sooty brown; clasper rather short and stout, with dermal denticles and pseudosiphon formed by dorsal dilatator muscle, without pseudorhipidion, with hook, promontory, rhipidion, sentinel, spike, shield and dike, dorsal marginal cartilage without distal extension, dorsal terminal 1 strap-shaped, dorsal terminal 3 joining tip of axial, two accessory terminal cartilages, ventral terminal with anterior notch; rostral base relatively broad, rostral shaft very slender, segmented and reaching rostral node and appendices, rostral appendices elongated, flattened over length and separated from shaft over most of length, propterygia of pectoral fins reach rostral node and appendices; nasal capsules of moderate size, rhomboidal in shape, without basal fenestra, internasal septum broad, nasal capsules not bulging me-

dially, anterior fontanelle and internarial distance moderately broad, interorbital width narrow, preorbital processes well developed, jugal arches moderately slender; scapulocoracoid little expanded anteroposteriorly, without anterior bridge and with only one postventral foramen.

*Species.*—*Breviraja colesi* Bigelow and Schroeder, 1948; *B. spinosa* Bigelow and Schroeder, 1950.

### *Neoraja* new genus

*Type Species.*—*Breviraja caerulea* Stehmann, 1976, here designated.

*Description.*—Rajoids with moderate to small size thorns along inner margin of orbits, over scapular and nuchal region (but not forming distinct triangular patch), along midline of disc in one or three distinct rows and along tail in one or three rows; upper surface more or less evenly covered with denticles; snout angular to obtusely rounded, tip of snout with a short and broad process, anterior margin of disc nearly straight to strongly concave, outer margins broadly to abruptly rounded, posterior margin broadly rounded; pelvic fins deeply incised, anterior lobes long (nearly equal in length to posterior lobes), narrow and bluntly to acutely pointed; tail relatively narrow proximally, long (generally greater than 60% of total length), with two small dorsal fins, with a dorsal and often a ventral caudal lobe; with or without oronasal pits; dorsal surface plain, mottled with irregular blotches, or marked with small dots; ventral surface whitish or whitish with dark colored blotches; claspers moderately to very long and slender, occasionally with dermal denticles but without pseudosiphon, without pseudorhipidion, with or without terminal bridge, with flag, rhipidion, sentinel, spike, shield, dike and funnel; dorsal marginal cartilage with free distal extension entering glans, with or without dorsal terminal 1, dorsal terminal 3 joining tip of axial, two accessory terminal cartilages, ventral terminal with or without anterior notch; rostral base relatively narrow, rostral shaft very slender, tapered, segmented and failing to reach rostral node; rostral appendices elongated, conical and separated from rostral shaft over most of length, propterygia of pectoral fin reaching rostral node and appendices; nasal capsules large, diagonally situated and ovoid in shape, with or without basal fenestrae, internasal septum moderately to very narrow, anterior fontanelle and internarial distance narrow, interorbital width narrow, preorbital process poorly developed; jugal arches very slender; scapulocoracoid little to moderately expanded anteroposteriorly, without anterior bridge and with one to several postventral foramina.

*Subgenera.*—*Neoraja* n. subg. and *Fenestraja* n. subg. *incertae sedis Neoraja mamillidens* (Alcock, 1889).

### *Neoraja* new subgenus

*Type Species.*—Same as genus *Neoraja*.

*Description.*—*Neoraja* species with small sized thorns along inner margin of orbits, over scapular and nuchal region, along midline of disc and tail in one row; snout obtusely rounded, outer and posterior margins of disc broadly rounded; pelvic fins with moderately long anterior lobes (equal to about 75% of length of posteior lobes) bluntly pointed; tail moderately long (about 60% of total length); caudal fin with small ventral lobe; without oronasal pits; dorsal surface more or less plain brownish-grey or bluish-grey, ventral surface whitish with brownish-grey blotches or margin; claspers moderately long and slender, with dermal den-

ticles, terminal bridge; dorsal terminal 1 cartilage with an anterior projection, ventral terminal with anterior notch; nasal capsules without basal fenestrae, internasal septum moderately narrow, scapulocoracoid with elevated rear corner, moderately expanded anteroposteriorly, with single postventral foramen; 23 to 27 trunk and 65 to 74 predorsal caudal vertebrae.

*Species.—Neoraja stehmanni* (Hulley, 1972), *N. caerulea* (Stehmann, 1976) and *N.* sp.

### *Fenestraja* new subgenus

*Type Species.—Raja plutonia* Garman, 1881, here designated.

*Description.—Neoraja* species with moderately to small sized thorns along inner margin of orbits, over scapular and nuchal region, along midline of disc and tail in one or three rows; snout angular to obtusely rounded, anterior margin nearly straight to strongly concave, outer margins broadly to abruptly rounded; anterior lobes of pelvic fin long (greater than 75% of length of posterior lobe) acutely pointed; tail with or without ventral caudal lobe; with oronasal pits; dorsal surface plain, mottled with irregular blotches or marked with small dots; ventral surface whitish; clasper very long and slender, without dermal denticles and terminal bridge; dorsal terminal 1 cartilage lacking, ventral terminal check-shaped without anterior notch; nasal capsules with basal fenestrae, internasal septum moderately to very narrow, scapulocoracoid little to moderately expanded anteroposteriorly, with one to several postventral foramina; 20 to 25 trunk and 64 to 76 predorsal caudal vertebrae.

*Species.—Neoraja plutonia* (Garman, 1881), *N. sibogae* (Alcock, 1889), *N. atripinna* (Bigelow and Schroeder, 1950), *N. cubensis* (Bigelow and Schroeder, 1950), *N. sinusmexicanus* (Bigelow and Schroeder, 1950) and *N. ishiyamai* (Bigelow and Schroeder, 1962).

## Materials Examined

*Breviraja atripinna:* Holotype MCZ 36370 (1) 23°22'N, 79°53'W, 594 m; MCZ 41828 (4) 23°40'N, 79°18'W, 530 m. *B. caerulea:* Paratypes ISH 720/74 (2) 57°41'N, 15°49'W, 1125 m. *B. colesi:* Holotype MCZ 36374 (1) 23°12'N, 81°23'W, 521 m; MCZ 36372 (1) 22°07'N, 81°08'W, 494 m; MCZ 36498 (1), 22°07'N, 81°08'W, 375 m; MCZ 36499 (1) 22°12'N, 81°11'W, 348 m; MCZ 41158 (1) 22°50'N, 79°18'W, 411 m; MCZ 41162 (1) 22°50'N, 79°08'W, 366 m; MCZ 41172 (1) 22°55'N, 79°16'W, 43 m; MCZ 41998 (4) 23°34'N, 79°07'W, 457 m. *B. cubensis:* Holotype MCZ 36443 (1) 23°21'N, 79°59'W; MCZ 41928 (2) 24°48'N, 79°17'W, 549 m. *B. ishiyamai:* Holotype USNM 196447 (1) 13°18'N, 82°12'W, 640 m; UMML 31682 (6) 26°24.1'N, 79°35.7'W, 738 m; MCZ 40097 (1) 13°56'N, 81°50'W, 503 m; MCZ 40665 (1) 24°11'N, 21°50'W, 732 m; MCZ 41829 (1) 26°39'N, 79°30'W, 732 m; MCZ 41834 (5) 24°24'N, 80°00'W, 732 m; MCZ 42446 (2) 24°12'N, 83°32'W, 914 m. *B. plutonia:* Holotype MCZ 914 (1) 31°N, 78°W; MCZ 41170 (4) 24°33'N, 83°34'W, 366 m; TCWC 2602.1 (6) 30°54'N, 79°49'W, 320 m; TCWC 2727.1 (2) 32°23'N, 76°34'W, 490 m; TCWC 2728.1 (4) 32°59'N, 77°14'W, 463 m; TCWC 2733.1 (2) 32°44'N, 76°49'W, 732 m; TCWC 2734.1 (2) 31°02'N, 79°48'W, 256 m; TCWC 2737.1 (2) 29°20'N, 79°50'W, 549 m; VIMS 2530 (1) 34°14'N, 75°54'W, 360 m. *B. sibogae:* Lectotype ZMA 113.491 (1) 07°15'S, 115°16'E, 289 m; Paralectotype ZMA 112.640 (1) 07°15'S, 115°15'E, 289 m. *B. sinusmexicanus:* Holotype USNM 103376 (1) 28°34'N, 86°48'W; MCZ 93742 (7) 29°10'N, 88°07'W; FSM 2349 (2) 29°30'N, 86°56'W, 348 m; TAMU 6-0134 (2) 21°16'N, 95°52'W, 567 m; TCWC 2696.1 (2) Gulf of Mexico, 366 m; TCWC 2698.1 (3) 19°38'N, 92°39'W, 494 m; TCWC 2704.2 (1) 28°49'N, 86°38'W, 443 m; TCWC 2721.1 (1) 21°16'N, 96°52'W, 548 m; TCWC 2724.1 (1) 27°01'N, 84°52'W, 366 m; TCWC 2729.1 (1) 27°40'N, 94°50'W, 640 m; TCWC 2730.1 (1) Gulf of Mexico; TCWC 2738.2 (1) 28°15'N, 86°06'W, 589 m. *B. spinosa:* Holotype MCZ 36373 (1) 30°58'N, 79°34'W, 457 m; MCZ 40200 (9) 16°43'N, 82°44'W, 503 m; MCZ 40232 (13) 16°42'N, 82°36'W; MCZ 42418 (1) 07°34'N, 54°13'W, 366 m; FSM 23846 (2) 25°03'N, 80°01'W, 412 m; TCWC 2601.1 (1) 30°30'N, 80°03'W, 274 m; TCWC 2695.2 (2) 12°52'N, 70°43'W, 512 m; TCWC 2727.2 (2) 32°23'N, 76°34'W, 490 m; TCWC 2728.2 (4) 32°59'N, 77°14'W, 463 m; TCWC 2732.1 (1) 32°45'N, 77°06'W, 549 m. *B. stehmanni:* SAM 26638 (1);

SAM 26639 (1) 33°S, 17°E. *B. yucatanensis:* Holotype USNM 148273 (1) off Yucatan, 422 m. *B.* sp: TCWC 2725.1 (1) 33°56'N, 75°54'W, 695 m; TCWC 2740.1 (1) 34°22'N, 75°43'W, 805 m. *Raja (Leucoraja) clarki:* Holotype USNM 156712 (1) 28°32'N, 86°20'W, 476 m; TCWC 2703.1 (2) 27°35'N, 92°59'W, 279 m. *R. (L.) erinacea:* TCWC 2742.1 Gulf of Maine. *R. (L.) ocellata:* VIMS 2354 (1) 44°45'N, 57°43'W, 37 m. *R. (Malacoraja) fuliginea:* Holotype USNM 163367 (1) 27°32'N, 93°02'W, 777 m; USNM 278057 (3) 28°12'N, 86°09'W, 722 m; TCWC 2701.1 (4) 27°26'N, 94°05'W, 1280 m. *R. (M.) nigerrima:* SOSC LWK 66-25 (6) 34°07'S, 72°19'W, 750 m; SOSC LWK 66-60 (1) 24°30'S, 70°40'W, 950 m. *R. (M.) senta:* VIMS 1538 (1) 43°19'N, 61°09'W, 128 m. *R. (Rajella) bigelowi:* Holotype USNM 218284 37°o5'N, 74°20'W, 1719 m. *R. (R.) fyllae:* SOSC 71°08'N, 31°53'E, 235 m.

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## Literature Cited

Alcock, A. W. 1889. Natural history notes from H. M. Indian marine survey steamer "Investigator", Commander Alfred Carpenter, R. N., D. S. O., commanding No. 13. On the bathyhial fishes of the Bay of Bengal and neighbouring waters, obtained during the seasons 1885–1889. Ann. Mag. Nat. Hist. (6)4: 376–399, 450–461.

Bigelow, H. B., and W. C. Schroeder. 1948. New genera and species of batoid fishes. J. Mar. Res. 7: 543–566.

———. 1950. New and little known cartilaginous fishes from the Atlantic. Bull. Mus. Comp. Zool., Harvard Univ. 103: 385–408.

———. 1953. Fishes of the western North Atlantic, Part 2. Sawfishes, guitarfishes, skates, rays, chimaeroids. Mem. Sears Found. Mar. Res. 588 pp.

———. 1954. A new family, a new genus, and two new species of batoid fishes from the Gulf of Mexico. Breviora Mus. Comp. Zool., Harvard Univ. (24): 1–16.

———. 1962. New and little known batoid fishes from the Western Atlantic. Bull. Mus. Comp. Zool., Harvard Univ. 128: 162–244.

———. 1965. Notes of a small collection of rajids from the sub-Antarctic region. Limn. Oceanogr. 10, suppl., pp. R38–R49.

de Buen, F. 1959. Notas preliminares sobre la fauna marina preabimal de Chile, con description de una familia de rayas, dos generos y siete especies nuevos. Boletin Mus. Nac. Hist., Santaigo 27: 173–201.

———. 1960. Tiburones, rayas y quimeras en la Estacion de Biologia Marina de Montemar, Chile. Revista Biol. Mar., Valparaiso 10: 3–50.

Forster, G. R. 1967. A new deep-sea ray from the Bay of Biscay. J. Mar. Biol. Ass. U. K. 47: 281–286.

Garrick, J. A. F. 1954. Studies on New Zealand Elasmobranchii. Part I. Two further specimens of *Arhynchobatis asperrimus* Waite (Batoidei), with an account of the skeleton and a discussion on the systematic position of the species. Trans. Royal Soc. New Zealand, 82: 119–132.

Hecht, M. K., and J. L. Edwards. 1977. The methodology of phylogenetic inference above the species level. Pages 3–51 *in* M. K. Hecht, P. C. Goody, and B. M. Hecht, eds. Major patterns in vertebrate evolution, Plenum Press.

Henning, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana, Ill. 263 pp.

Hubbs, C. L., and R. Ishiyama. 1968. Methods for the taxonomic study and description of skates (Rajidae). Copeia 1968: 483–491.

Hulley, P. A. 1970. An investigation of the Rajidae of the west and south coasts of southern Africa. Ann. S. Afr. Mus. 55: 151–220.

———. 1972a. The origin, interrelationships and distribution of southern African Rajidae (Chondrichthyes, Batoidei). Ann. S. Afr. Mus. 60: 1–103.

———. 1972b. A new species of southern African brevirajid skate (Chondrichthyes, Batoidei, Rajidae). Ann. S. Afr. Mus. 60: 253–263.

———, and M. Stehmann. 1977. The validity of *Malacoraja* Stehmann, 1970 (Chondrichthyes, Batoidei, Rajidae) and its phylogenetic significance. Ann. S. Afr. Mus. 72: 227–237.

Ishiyama, R. 1952. Studies on the rays and skates belonging to the family Rajidae, found in Japan and adjacent regions. 4. A revision of three genera of Japanese rajids, with descriptions of one new genus and four new species mostly occurring in northern Japan. J. Shimonoseki Coll. Fish. 2: 1–34.

———. 1958. Studies on the rajid fishes (Rajidae) found in the waters around Japan. J. Shimonoseki Coll. Fish. 7: 1–394.

———. 1967. Fauna Japonica, Rajidae (Pisces). Tokyo Electrical Engineering College Press, Toyko, Japan. 84 pp.

———, and C. L. Hubbs. 1968. *Bathyraja*, a genus of Pacific skates (Rajidae) regarded as phyletically distinct from the Atlantic genus *Breviraja*. Copeia 1968: 407–410.

Krefft, G. 1968. Neue und erstmalig nachgewiesene Knorpelfische aus dem Archibenthal des Sudwestatlantiks, einschliesslich einter diskussion einiger *Etmopterus*-Arten sudlicher Meere. Arch. FischWiss. 19: 1–42.

McEachran, J. D. 1977. Variation in *Raja garmani* and the status of *Raja lentiginosa* (Pisces: Rajidae). Bull. Mar. Sci. 27: 423–439.

———, and L. J. V. Compagno. 1979. A further description of *Gurgesiella furvescens* with comments on the interrelationships of Gurgesiellidae and Pseudorajidae (Pisces, Rajoidei). Bull. Mar. Sci. 29: 530–553.

———, and C. O. Martin. 1978. Interrelationships and subgeneric classification of *Raja erinacea* and *R. ocellata* based on claspers, neurocrania and pelvic girdles (Pisces: Rajidae). Copeia 1978: 593–601.

———, and J. A. Musick. 1973. Characters for distinguishing between immature specimens of the sibling species, *Raja erinacea* and *Raja ocellata* (Pisces: Rajidae). Copeia 1973: 238–250.

Menni, R. C. 1972. *Raja* (*Atlantoraja*) subgen. nov. y lista critica de los Rajidae Argentinos (Chondrichthyes, Rajiformes). Fac. Ciencias Naturales UNLP (Nueva Serie) 11(103): 165–173.

Stehmann, M. 1970. Vergleichend morphologische und anatomische Untersuchungen zur Neuordnung der Systematik der nordostatlantischen Rajidae. Arch. FischWiss. 21: 73–164.

———. 1976a. Revision de Rajoiden-Arten des nordlichen Indischen Ozean und Indopazifik (Elasmobranchii, Batoidea, Rajiformes). Beaufortia 24: 133–175.

———. 1976b. *Breviraja caerulea* spec. nov. (Elasmobranchii, Batoidea, Rajidae); eine neue archibenthale Rochenart und zugleich ein Erstnachweis ihrer Gattung im Nordostatlantik. Arch. FischWiss. 27: 97–114.

———. 1977. Ein neuer archibenthaler Roche aus dem Nordostatlantik, *Raja krefftі* spec. nov. (Elasmobranchii, Batoidea, Rajidae), die zweite Spezies im Subgenus *Malacoraja* Stehmann, 1970. Arch. FischWiss. 28: 77–93.

———. 1978. Illustrated field guide to abundant marine fish species in Argentine waters. Mitteilungen aus dem Inst. fur Seefischerei, Hamburg. 23: 1–114.

Vaillant, L. 1888. "Poissons." *In:* Expeditions Scientifiques du 'Travailleur' et du 'Talisman' pendant les annees 1880–83. Paris. 406 pp.

Weber, M. 1913. Die Fische der Siboga-Expedition. Monogr. Siboga Exped. 57: 1–710.

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